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REACTIONS OF VARIOUS PLANKTON ANIMALS WITH REFERENCE TO THEIR DIURNAL MIGRATIONS

BY

CALVIN O. ESTERLY

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INTRODUCTION

This paper reports the results of a year of study on the behavior of some marine plankton organisms. The chief aim of the work was to ascertain the factors that determine the diurnal migrations of such forms. It was outside my purpose to attempt to learn how sensitive the animals under experiment might be toward changes in surrounding factors such as light or temperature, for example. It was not in the plan, furthermore, to consider questions connected with the interpretation of behavior as applied to such matters as the mechanism of orientation. The end desired was to learn how the direction of movement is affected by various external conditions. The actual experimental facts were sought rather than the laws or principles underlying them. Since the experimental work was not concerned with the physiology of the movements controversial matters connected with that phase of the study of behavior are not discussed.

It is important that it be understood that this investigation of responses was undertaken with the definite end in view of obtaining a basis for explaining habits in nature. The natural conditions experienced by the animals in the course of the vertical movement were constantly considered, and the mode of procedure was based on that consideration. In general, it may be said that during descent the temperatures encountered are progressively lower, and during ascent

the animals pass into warmer and warmer water. From the surface to a depth of about thirty meters there is a slight decrease in salinity, but from thirty meters down the salinity gradually increases. The light intensity during the day grows less as the distance beneath the surface increases; this is probably true for the night also; but for that time the difference in degree of illumination at the surface and at lower levels is so much less than during the day that it is practically negligible, unless phosphorescence makes light that is more intense below the surface. Since plankton animals are commonly found in deeper water by day and nearer the surface by night, they pass through a range of temperatures and densities as they move up and down. Furthermore, during the day they are in water of higher salt concentration and lower temperature and in light of relatively low intensity, compared with the surface. While the illumination at the surface is low during the night also the temperature is higher and the salinity lower than the animals encounter by day, although forms that do not descend during the day farther than about thirty meters will be in water of less salinity than at the surface.

Now if natural surroundings are to be simulated in experiments conducted for the purpose already mentioned, it is a comparatively simple matter so to arrange conditions that if the animals move downward they meet with lower temperature, higher salinity, and decreased light intensity, or with the reverse of these three conditions if they ascend. It is needless to point out that there are some oceanic conditions that can not be reproduced in the laboratory, such as great depth of water, tidal currents, or distance from shore. But it is easy to provide a temperature gradient with cold water at the bottom of a column. If a light is placed at the top of the column the intensity will be greatest at the surface and progressively less below the surface. Or it may be arranged that cold water of higher salinity shall be found at the lower part of a cylinder where the light intensity is measurably less than toward the top. On the other hand, experimental conditions can be secured in the laboratory which would not be met by the organisms in the sea. An example of this is lighting a vertical container from below. It is permissible, of course, to introduce unnatural conditions but only for the purposes of interpreting activities observed under the more natural conditions. On the whole, however, the experimental conditions were patterned after the general oceanic environment as regards light, temperature, and salinity.

This experimental study of diurnal migration was undertaken only after a number of years of field investigation by the Scripps Institu-

tion. Such work has shown, we believe, that the vertical movement is wide spread among plankton organisms found in the San Diego region, and that the conditions and factors involved make a problem of great complexity. Studies of the field records indicate that it is possible to ascertain without recourse to experiment some of the relations existing between external conditions and the movements of the animals. Such studies, as carried on at the Institution, involve a large amount of statistical and mathematical work (Michael, 1916, p. xix). It is difficult to carry on the field and experimental work at the same rate, so that experimental results will be considered for the most part at this time. Some papers have already appeared dealing with the field results (Michael, 1911, 1913, Esterly, 1911, 1912) and others are in course of preparation. The published papers are based on statistical methods that as a rule give trustworthy and significant results. In some cases, however, the field data are inconclusive, and the experiments were not completed on some of the forms. It has seemed desirable, nevertheless, to point out in this paper the possible relation between the experimental results and the behavior in the sea as we understand it from our field data. Statements about this relation are more or less speculative, however, since both the field and experimental data are lacking in certain respects.

METHODS AND MATERIAL

The laboratory procedure and apparatus were purposely as simple as possible. Most of the work was done in a room with black walls. Daylight entered the room through a north window 50 by 40 cm., and this area could be reduced by means of a curtain and shutters of different sizes. Artificial light was obtained from Mazda lamps. The lamp in use was enclosed in a housing of black sheet iron. The rays from the bulb passed out through a filter of Corning "Daylite" glass, which according to Gage (1915) gives the electric light a quality closely approaching that of daylight. The lamps were 15-watt and 100-watt, the latter gas-filled and with a concentrated C-shaped filament; the opening in the housing of the former was 38 mm., in diameter, of the latter 46 mm. The relative intensities of the different light were determined roughly by means of a method suggested by Dr. G. F. McEwen. Two blocks of paraffine of the same thickness were clamped together with opaque cardboard between. The blocks were placed between the lights to be compared and by suitably varying the distance of the light from the paraffine it was possible to obtain approximately

equal illumination on the two sides of the cardboard screen. The light is diffused by the paraffine to such an extent that the edges of the blocks show when both are equally lighted. The 15-watt lamp was used as a standard of intensity. The intensity of the 100-watt is about 6, if that of the other lamp is called unity. The 50 by 40 centimeter window gives an intensity about 3800 times that of the 15-watt, and 400 times that of the 100-watt. These figures are only approximations, of course, but they serve for present purposes.

Temperatures lower than those ever found at the surface of the sea in the region about La Jolla were produced by putting a dish or tube of sea water into ice. With a vertical container the whole column or only the lower portion could be cooled, the latter case giving a gradient with a difference of 8°C or 10°C between the top and bottom.

Water of a salinity greatly above that of ordinary sea water was obtained by allowing evaporation to continue for days in a warm room. This highly concentrated water was diluted with normal ocean water until a desired degree of salinity was reached. The actual salinity was computed by means of Knudsen's tables (1901) from the specific gravity as given by a hydrometer. It should be noted that this method of increasing the salinity does not involve changing the relative proportions of the salts in sea water as does the addition of one salt, such as NaCl, to ordinary sea water. I did not attempt in any case to ascertain whether a decrease in the salinity has an effect on reactions.

In many experiments a single animal was enclosed in a glass tube 500 by 30 mm., which was filled with water and closed with a rubber stopper so that no air space remained. The tube could be clamped to a ring support and held in position so that light might enter from above or from below; or the tube could be kept horizontal. It is possible, furthermore, to arrange the test so that the animal must start at the top or at the bottom of the column of water, by swinging the tube through 180°. There was no apparent effect on the animals from the mechanical stimulus caused by turning the tube; if there was it could not have been as great as that caused by picking up the specimen in a pipette.

All the animals were collected by means of a conical plankton net. A wide-mouth bottle or jar was tied into the peak of the net, so that the organisms were never out of water and they were not handled at all until in the laboratory. It was found that the specimens were in better condition and lived longer if they passed from the net into a large amount of water, and accordingly, for the greater part of the collecting a two-quart jar was tied into the net.

The animals were kept in a large glass dish in the laboratory; and as a rule individuals were picked out of this stock as needed, and thereafter each one was kept in a finger bowl. Some species could be kept alive for a week, but most of the forms did not withstand laboratory conditions well. While I thought at the beginning that it would be desirable to test each one of a given set of individuals for several days, if possible, that plan was soon abandoned, and many, if not most of the experiments were performed with animals collected during the morning of the day on which they were used, or during the preceding night. But if specimens appeared to be in good condition on the second day I did not hesitate to use them. The precautions taken to have fresh material are not necessary, in my experience, to guard against alterations in the form of the responses. I believe that there is something connected with laboratory conditions that does affect the reactions of some species so that there is a change after the animals are removed from the ocean. But if the change occurs it appears shortly or within a few hours after the animals are brought in. Results are uniform after that, so far as sign of reaction is concerned, as long as there is any response.

The water in which the animals were kept after collection was either that from the laboratory system or it was brought into the laboratory from the end of the pier (1000 feet from shore) in glass jars. So far as I could determine from a large number of trials with different species, the behavior is practically the same in water from the two sources; though I believe that the animals remain in better condition and live longer if they are not put into water that has passed through the pipes of the pumping system.

The experiments were carried on with adults of the following forms: the copepods *Acartia tonsa* and *A. clausi, Calanus finmarchicus, Eucalanus elongatus, Labidocera trispinosum, Metridia lucens,* and the chaetognath *Sagitta bipunctata.* It was originally intended to carry out the same series of tests with specimens of each species, but this proved impossible. The chief reason is that some species were not obtained in sufficient numbers or long enough through the year. *Acartia tonsa, Calanus,* and *Sagitta* could be counted on at almost any time, and were obtained in fair abundance, but the other species were more or less erratic in occurrence. There were times, indeed, when collecting was uniformly unsuccessful, even *Acartia* being absent from the surface at night though ordinarily very abundant then. The collections varied from time to time, also, so that it was necessary to use different species on different days as they happened to come.

LITERATURE

The first investigators to study diurnal migration from the experimental side were Groom and Loeb (1890). They worked with the larvae of a barnacle, *Balanus perforatus*. Their general conclusion (p. 173) is that the animals move down because they are negative toward the intense light of day, while they ascend at night because they are at least not negative to light of the intensity that prevails then. The authors consider that their experiments show ". . . dass die ganze Erscheinung der periodischen täglichen Tiefenwanderung der Tiere eben nur dadurch möglich ist, dass dieselben erstens heliotropisch sind, das heiszt, dass sie durch den Lichtstrahle gerichtet werden; und zweitens, dass der Heliotropismus. . . Abends (im schwachen Licht) positiv, am Morgen (bei starkem Licht) negativ ist." They state, however (p. 176) that the matter is different with certain copepods; they could not establish that there is a change in heliotropism in these forms.

A few years later Loeb (1893) studied several different kinds of smaller pelagic animals. *Polygordius* larvae are made positively heliotropic by cooling, and negative by warming (p. 90). Increase of concentration (by adding NaCl to sea water) has the same effect as cooling, while decreasing the concentration by adding fresh water to sea water causes the negative response (p. 94). Copepods, "probably Temora longicornis" are affected the same way as the worm larvae (p. 96). Loeb states (p. 104) that he has worked with copepods, larval crustacea, worms and mollusks, and has not found a pelagic animal of these sorts that would not become permanently or temporarily positive to light under certain conditions. Geotropism, however, as well as light has some effect in determining the vertical distribution since positive heliotropism and negative geotropism and negative heliotropism and positive geotropism work in the same direction (p. 105). A number of years later (Loeb, 1906) it was found that copepods are made positively heliotropic by CO_2 or any dilute acid (p. 565), as is *Daphnia* (p. 568). Fresh water *Gammarus* also is made strongly positive, but this condition endures only a few seconds (p. 570). The larvae of *Balanus* become positive in water to which carbon dioxide is added (p. 575).

A general statement of the bearing of such experimental results on the migration was given by Loeb in 1908. He regards light as

perhaps the most important factor (p. 732). "Diese periodischen Tiefenwanderungen der pelagischen Organismen führten wir darauf zurück, dass aüssere Umstände einen periodischen Wechsel im Sinne des Heliotropismus derselben bestimmt. . . ." Acids and temperature are among the external conditions that affect the sign of heliotropism, and the application of such facts to diurnal movement is as follows (p. 733): As the animals descend they must reach colder water, and finally they encounter temperatures in which they become positively heliotropic; this checks the descent and brings about an upward movement. Since the temperature of the water nearer the surface decreases toward evening, the animals must reach higher and higher levels and ultimately the surface in consequence of the continuance of the positive heliotropism. As long as the temperature at the surface is sufficiently low the animals do not descend; but as morning advances the surface water becomes warmed, the positive heliotropism disappears, the active upward swimming ceases, and the animals sink or swim down. Then, as before, the descent is checked by low temperature at some level and the upward movement begins again. The fact that acids, especially carbon dioxide, cause positive heliotropism is also applicable to diurnal migration, particularly in fresh water animals. The carbon dioxide content of the water must diminish during the morning since the aquatic plants are consuming it in the manufacture of starch; and this decrease in carbon dioxide causes positive heliotropism to lessen in intensity. The animals, consequently, descend either by sinking or swimming, since they no longer make efforts to swim toward the light. As the light begins to wane in the latter half of the day the carbon dioxide gradually increases in amount up to a point where positive heliotropism is induced. Furthermore, light itself alters the sign of heliotropism (p. 734). Very intense light has a tendency to make certain forms negative, and the violet and ultra-violet rays have this effect also. This must mean that pelagic animals will descend by day and ascend by night. In addition, geotropism and viscosity of the water are factors that enter into depth migrations.

This paper of Loeb's (1908) has something of a controversial tone as regards certain statements by Bauer (1908), chiefly as to whether reactions to vertical and horizontal rays are similar. Without going into the question, it is sufficient to note here that Loeb (1908, p. 735) states that he has worked on thousands of positively heliotropic forms and has always found them to be positive to vertical as well as to horizontal light.

As recently as 1913 Loeb reiterated the same general views as to the factors that are concerned in the migration. He mentions the effects of temperature and carbon dioxide, and in addition suggests (p. 480) that "die durch das Light bestimmten chemischen Prozesse auf die Dauer ebenfalls den Sinn des Heliotropismus beeinflussen in der Weise, dass längerer starke Beluchtung die Tendenz zur Indifferenz oder zu negativem Heliotropismus erhöht während länger andauernde schwache Beleuchtung die Tendenz zu positivem Heliotropismus erhöht." A fourth factor, possibly, is found in periodic variations in the internal chemical processes. "Wenn diese Schwankungen des chemischen Prozesses dem Wechsel von Tag und Nacht entsprechen (man denke an die nyktitropen Bewegungen der Pflanzen), so könnten sie auch periodische Tiefenwanderungen induzieren."

I think it is a fair statement of Loeb's views that change in heliotropism because of change in external conditions is the principal factor in the periodical depth migration. It would be well to note, also, that this seems to be regarded by Loeb as of general application, though he does not say so. His aim, however, evidently is to find a simple and general explanation for the habit.

The views of Loeb regarding diurnal migration do not meet with the unqualified approval of Bauer (1908). The disagreement between these writers has been impartially discussed by Burckhardt (1910). Bauer studied the movements of various Mysidae, and he insists that these animals do not react to horizontal light as they do to vertical rays. He also has this to say (p. 368) with regard to the periodic depth migration: "Die Erklärung der Tiefenwanderung planktonischer Organismen durch positive oder negative Phototaxis (geprüft mit der üblichen Anordnung für Phototaxisversuche) isht daher ein methodische Fehler." Later, in replying to Loeb (1908), Bauer (1909, p. 79) states that his only criticism was directed chiefly against the practice of applying to the migration problem the results obtained in experiments with horizontal light without further evidence as to the behavior in vertical lighting, since the light comes from above in the natural habitat of the animals.

The well known work of Parker (1902) on the copepod *Labidocera aestiva* is an example in which experimental results clearly reveal possible reasons for the diurnal movement. Parker believes that the behavior observed by him in the laboratory "undoubtedly imitated in miniature the natural daily mirations of female Labidocerae in the sea" (p. 119). The migrations of the animals are explained as follows

(p. 123): "Females rise to the surface with the setting of the sun, because they are positively phototropic to faint light and negatively geotropic; they descend into deep water with the rising of the sun, because they are negatively phototropic to strong light (their negative geotropism being overcome by their negative phototropism); the males follow the females in migration, because they are probably positively chemotropic toward the females." Parker notes (p. 122) that such an explanation need not apply to other plankton organisms, although their depth migrations may be made at the same time as those of *Labidocera*.

The important paper by Dice (1914) deals with the reactions of *Daphnia* and their bearing on the vertical movements. These careful and thorough experiments led Dice to conclude (p. 263) that "the diurnal movements of *Daphnia pulex* are caused chiefly by variations in geotaxis induced by changes in light intensity." Increase of intensity leads toward positive geotropism, decrease toward negative geotropism. Temperature also has an effect, since high temperatures tend to make the animals positively geotactic, while low temperatures have the opposite tendency. Dice gives (p. 262) the results of the experiments of others that may be taken to show that reversal of geotropism by changes in light and temperature occurs in other forms.

Another point of view, as regards the causes of the diurnal movement, is that of Ewald (1910, 1912). His laboratory observations on the behavior of Cladocera and of *Balanus* larvae led him to the conclusion that while light is an important factor it is not necessary to hold that there is continually recurring alternation between positive and negative heliotropism. The forms that Ewald used show what he called locomotion periods; these are, objectively, alternate ascents and descents. If the light is too intense, the animals cease their locomotion movements and therefore sink, and when they reach a region of lower intensity the swimming begins again. There are, therefore, successive periods of inhibition and stimulation (Ewald, 1912, p. 609) which have the effect of maintaining the animals in regions of about equal illumination all day long; they ascend in the evening and descend in the morning without giving positive and negative heliotropic reactions.

There is still another possible factor that may determine the diurnal movement. This is the effect of a physiological or metabolic rhythm. Such a factor has not received general consideration, but Menke (1911) makes much of it from his point of view. His experi-

mental work was done with the arthropod *Idothea*. He found that there is a periodical change in the chromatophores corresponding to day and night; the animals are darker by day than by night (p. 43). Menke formulates the proposition (p. 57) that variation in light intensity acts as a regulating mechanism. If external conditions are kept constant the chromatophores contract and expand corresponding to the usual periodicity of light and darkness. He was even able to reverse the rhythm, so that the old rhythm was set aside, by lighting the animals at night and keeping them in darkness by day. After nine days of this they were kept in constant darkness, and for about a week the pigment cells contracted by day and expanded at night. Menke cites other facts that show that there is a periodicity of metabolism: the animals are livelier at night and the heart beats twice as fast as by day (pp. 64–66), and, furthermore, agents such as temperature and acids affect the movements of the chromatophores.

Such facts are applied by Menke (pp. 79–80) to the vertical migrations of plankton animals. He notes that the heliotropism of such forms has been shown to be reversed by temperature changes, which in turn affect the chemical processes, and he says (p. 80): "In weiterer Verfolgung dieses Gedankenganges wird man zu den Schluss gedrängt, dass die primäre Ursache Vertikalwanderung mancher planktonischer Organismen in Stoffwechseländerungen legt, und dass erst sekundär mit diesen chemischen Prozessen ein heliotropischer Stimmungswechsel verkettet ist." The periodical migrations and the periodicity of chromatophore movements are occurrences of essentially like nature, conditioned by periodicity in metabolism. The same agents that affect pigment cells alter the heliotropism and in corresponding ways. Raising the temperature causes negative heliotropism in many animals and it also brings about contraction of the pigment cells. Lowering the temperature causes expansion of chromatophores and reverses the heliotropism to positive (p. 81). An interesting suggestion is made (p. 82) as to the regulatory character of the migration. The osmotic pressure of the body fluids is altered as the metabolic changes take place, and the animals move into regions of corresponding pressure to compensate for this.

In brief, the conclusion reached by Menke, as given on page 88, is that the movements of the chromatophores and those shown in the diurnal migration are "autonomous," and that they parallel a periodicity in metabolism which is probably characteristic of all living matter. The fact that the metabolic rhythm follows the daily changes

in light intensity is explained on the ground that specific chemical processes are set up under the influence of light or darkness, and that these processes "in iherer Art eben die Periode einer Erregung des Stoffwechsels resp. dessen Ruhe verursachen."

I believe that Menke's work has brought to light a factor that must be considered in the matter of the depth migrations. I have pointed out (Esterly, 1917*b*) that two species of *Acartia* exhibit a periodicity of behavior that is not connected at the time with recurring external stimuli; the same is true, though to a less extent, of *Calanus*. It remains to be determined by experiment how general this factor is.

The foregoing account of the literature has covered the papers that deal with depth migration more extensively from the experimental side. There are, in addition, some other references to this habit that may be mentioned. Harper (1907) showed that the insect larva, *Corethra,* is positively geotropic in strong light from above as well as in that from below, and that it is negatively geotropic in dim light. Harper suggests (p. 454) that the animals move down in the daytime because of positive geotropism in strong light, and that they ascend when the intensity decreases.

My own studies of the reactions of *Cyclops* (Esterly, 1907) were directed toward an understanding of diurnal movement. The females of *Cyclops albidus* were shown to be negatively geotropic in the dark and positive in the light, and it was suggested that phototropic responses are not even the main factors in causing the diurnal migrations. The effect of light on the geotropism, however, offers a possible explanation.

There are, of course, very many papers dealing with responses that might be applicable to the diurnal movement if the facts about natural distribution were known for those particular forms. But it does not seem desirable to include such accounts of behavior here. Similarly, the extended literature dealing with results derived from field investigations may be omitted since the purpose of this report is to give an account of a set of experiments on certain forms and of their possible bearing on the diurnal migrations of the same species.

In discussing the literature it would not be well to omit mention of the theories of Ostwald with regard to the diurnal movement. As is well known, the chief point in his theory is that the movement is largely due to alterations in the viscosity of the water, the viscosity in turn being dependent on the temperature. The migration of the animals is not so much due to their own activities as it is to the physical condition of the medium in which they live. Ostwald states,

however (for example, 1902, p. 627), that alterations of viscosity are not the only causes of vertical movements. Tropisms play a part but a subordinate one.

This is hardly the place to go more deeply into Ostwald's explanation, especially since my own experiments were along very different lines than those suggested by his work. It does not seem to me, however, that plankton organisms can be regarded as passive bodies that are carried up and down through physical agencies. Those forms that I have watched *swim* up when they ascend. Although they may drop down passively, this does not occur as a result of change of temperature so far as I can see; temperature has an effect but not in the way set forth by Ostwald.

In concluding the review of the literature, it seems necessary to note the somewhat unusual views expressed by Franz in a number of papers (1911, 1912, 1913). He holds that vertical migrations do not occur; that the reason for the larger number at the surface at night, as shown by collections, is that the animals can not see the nets then so as to avoid them. According to his view, the animals are really as abundant at the surface during the day as during the night but they escape the nets when it is light enough for them to see (1911, p. 10). I believe that the views Franz expresses are untenable so far as they relate to carefully conducted field investigations, but he has done well to point out that the results of laboratory experiment alone do not show what goes on in nature. For example (1913, p. 265) he states that in his opinion the observations concerning the phototaxis of *Balanus* larvae and similar forms do not offer any ground for assuming that plankton animals perform periodical vertical migrations. Phototactic phenomena in the laboratory give only a broken picture of behavior in the open. When he proceeds, however, to argue that because experimental results do not show what takes place in nature, the diurnal movement does not take place, he goes too far. He gives a good many reasons why laboratory phototaxis can not be identified with migration movements in the open and says (1912, p. 499): "Diese wohl einschneidende Kritik der Lehre der Phototaxis bei Tieren entzieht zugleich der Annahme von regelmässigen vertikalen Wanderungen der Planktontiere eine ihrer wichtigsten Stutzen." The phototaxis (in the laboratory) is at most a "flight movement" (fluchtbewegung) which can only be of short duration in the open. It will be noted that Franz passes from the statement that a supposed habit can not be explained in a particular way to the argument that, for such a reason, the existence of the habit is questionable.

CONDITIONS OF LIFE IN THE SEA

It is advisable to point out something of what is known about the physical conditions of the sea in the region where the work of the Scripps Institution has been carried on, since the experiments here considered relate especially to the behavior of animals found under those conditions. The recent paper of McEwen (1916) summarizes the knowledge of the conditions in the San Diego region, and the statements that follow are based on that paper. The points that I desire especially to emphasize are the *variations* in temperature, salinity, and light intensity.

It is stated (McEwen, 1916, p. 267) that the annual range of surface temperatures is between 6° and 7°C, the upper and lower limits varying somewhat in different areas. The lower limit is from 14° to 15° and the upper from 20° to 22°; the coldest months are February, March, and April; the warmest season is the month of August. The water contains less salt in the spring than during the summer. The salinity varies from 33.50 °/₀₀ in February to 33.75 °/₀₀ in July or August in one area; in another section the minimum is 33.55 °/₀₀ in January, the maximum 33.85 °/₀₀ in July or August. The annual range of temperature "decreases from 6°.2 C at the surface to 1°.0 C at two hundred meters, while it can scarcely be detected below four hundred meters" (p. 268). Different months differ as to the monthly average of temperature and salinity, as do different days of the same month; and "each year is distinct from the others" (p. 269). Furthermore, there are significant differences in temperature at positions as little as sixty feet apart (p. 269). The bearing of such facts on the field study of plankton organisms is obvious and is noted by McEwen on page 270.

The diurnal variation in environmental elements is of more importance than the seasonal so far as the daily vertical migration is concerned. It is stated (p. 271) that the diurnal range in surface temperature in a region well offshore is about 1°.0 C; the lower limit of the range occurs between 1 A.M. and 2 A.M., and the upper between 5 P.M. and 7 P.M. This slight diurnal variation decreases as the depth increases, and it does not appear at depths exceeding 25 meters.

The diurnal variation of salinity at the surface is given as about 0.05 °/₀₀ (p. 271).

It will probably be granted without argument that daily variations in surface temperature and salinity are too small to have a marked

effect in causing diurnal migration. But temperature and salinity vary with the depth, as is well known, so that the migration of the animals carries them through a greater range of temperature and salinity. McEwen has given in plates 34 and 35 the relations of the mean annual temperature and salinity to depth.

The maximum of the mean annual temperature (pl. 34) is at the surface of course, and is 17° C. At 25 meters it is between 14° and 15°; at 50 meters between 12° and 13°; at 100 meters between 10° and 11°; at 150 meters it is 10° C; while at 200 meters it is about 9°5 C. From that level it gradually decreases to 7°5 C at 400 meters. The temperature curve is much steeper between the surface and 100 meters than anywhere else.

The salinity increases with the depth (pl. 35), except that from the surface to about 25 meters there is a slight decrease. The mean annual salinity at the surface is 33.65 °/₀₀; at 25 meters it is between 33.50 °/₀₀ and 33.55 °/₀₀; at 50 meters it is about 33.57 °/₀₀; at 75 meters about 33.68 °/₀₀; and at 100 meters it is 33.80 °/₀₀. From that level to 200 meters the increase is at about the same rate for each 25 meters, the value of the salinity at the 200-meter level being 34.15 °/₀₀. The increase is less rapid from there down, and at 400 meters the percentage is a little in excess of 34.39 °/₀₀.

The light intensity at different depths has not been measured directly in the San Diego region, but McEwen has given approximations of the average distribution of radiant energy with respect to depth and time of day (pl. 38). The diagram is based on a formula that expresses the relation between intensity of radiation and depth and an "empirical one representing approximately the results of observations on the diurnal variation in the intensity of solar radiation on a horizontal surface at sea-level, between 20° N and 40° N" (p. 279). While McEwen's diagram gives theoretical results he states that the values agree well with photographic measurements made in the Atlantic.

According to the figures given in plate 38, if the intensity at a depth of one meter at noon is called 1000, it is relatively about 600 at nine meters, 300 at 20 meters, 200 at 25 meters, 100 at 35 meters, 50 at about 48 meters, 25 at 58 meters, 10 at a little over 70 meters, and 5 at 82 meters. It is doubtless understood that the light intensity at any depth increases until noon and decreases after noon, so that *time of day* is a rough expression of relative intensity.

EXPERIMENTAL RESULTS

Reactions of the Copepods *Acartia tonsa* and *A. clausi*

These little copepods are usually abundant at the surface at night. *A. tonsa* is found throughout the year, while *A. clausi* occurs chiefly or only during the winter and spring. If it is desired to obtain animals during the day it is almost always necessary to do the collecting in deeper water than is found along the pier at La Jolla. We were successful, as a rule, at depths of 60 to 100 feet. There have been sunny days, however, when both species were abundant on the surface. Sometimes they were not obtained at the surface at night. The relations between these unusual modes of distribution at the surface and external conditions have not been worked out, but it is expected that something will be ascertained about such matters from a study of the large number of collections and the mass of data already on hand.

PHOTOTROPISM

Evidence has been given in another place (Esterly, 1917*a*) that *Acartia tonsa* if taken from the surface is always positive to horizontal light of any intensity if the temperature of the water is over 15° C. There is a tendency for the negative reaction to appear in colder water. Animals that have come from twenty or thirty meters are negative to light if tested soon, but if they are kept in the laboratory such specimens give only positive responses after a time. *A. clausi* reacts as does *tonsa* in most respects: it is positive to light at temperatures above 15° C, but shows a larger proportion of negative responses in colder water (Esterly, 1917*a*). Most surface specimens of *clausi* when first taken are negative to horizontal light if they are tested in water below 15° C, but after some hours most animals have become positive. Both species give negative responses to horizontal light if the animals are obtained below the surface. It seems important to note, first, that if cooling has any effect on the reactions of these animals to light, it causes negative phototropism; second, that the behavior is in some way related to or dependent on the habitat from which the experimental specimens come; third, something connected with retention in the laboratory modifies the character of the responses to light.

GEOTROPISM

It has been shown (Esterly, 1917*b*) that *Acartia tonsa* and *A. clausi* have a marked tendency to remain at or near the top of a column of water when in the diffuse light of a room. And specimens of both forms are to be found largely toward the bottom when kept in the dark during the day. But from 6 P.M. to 8 P.M. they both show a noteworthy increase in the upper levels even if they have been for hours continually in darkness except for occasional observations. This rhythm is less marked in *tonsa* at temperatures below 16° C, but it is clearly shown in *clausi* at those temperatures. In view of the tables published in the paper cited it is unnecessary to repeat the figures here.

Acartia tonsa is positively geotropic if the animals are obtained in deep water and tested within a short time; nothing could be more striking by contrast with the surface animals than the way in which the others swim down in diffuse light, or from the 15-watt lamp at the top of a tube, or in darkness. Some details of experiments may be useful at this point, although my material dealing with the geotropism of deep-water *Acartia* is not sufficient to warrant tabulation.

On November 1, 1917, a haul from about 100 feet was brought into the laboratory at 11:30 A.M. Fifteen animals (eleven females and four males) were tested one by one and all were negative to light from the window of the dark room. Ten of these animals (the four males and six of the females) were put, one by one, into a vertical tube 50 by 3 cm., beginning at 2:30 P.M. They all swam to the bottom in the light of the north windows in the main room and all were at or close to the bottom when observations were taken at 2:40, 3:00, 3:30, and 4:20 P.M. The next observation was at 6:20 P.M.; at that time there were three animals at the top while at 7:20 there were five at the top.

Another lot of animals was obtained from about 120 feet on December 1, 1917, and was brought into the laboratory at 10:15 A.M. Eight animals were tested in the light of the large window in the dark room, by releasing each individual at the center of a shallow dish and noting the direction of travel. I have records for seventeen such trips, and only two were positive. The two were made by an animal that also made one negative trip. At 11:15 A.M. the animals were put into a vertical tube (50 by 3 cm.), one by one. The tube was left standing in the dark room one meter from the window. The length of the tube was marked off into five equal divisions, and in giving the distribution of the animals the number in the top section is set down at the left, and

so on, to the number in the bottom section, at the right. At 11:20 A.M. the distribution was 1, 1, 0, 0, 6; at 12:45 P.M. and 12:55 P.M. it was 0, 0, 0, 0, 8. Then the tube was turned horizontal, so that what was the lower section became the one next the window. The animals all swam away from the light, and when they were in the section opposite the window, the tube was turned to the vertical position, at 1:33 P.M. This brought all the specimens into the top section. The distribution at intervals follows: 1:35 P.M., 1, 1, 1, 2, 3; 1:37 P.M., 1, 0, 1, 1, 5; 1:38 P.M., 0, 1, 0, 1, 6; 1:39 P.M., 0, 1, 0, 0, 7; 1:40 P.M., 0, 0, 1, 0, 7; 1:41 P.M., 0, 0, 0, 1, 7; 1:42 P.M., 0, 0, 0, 0, 8. At this point the room was made dark and the 15-watt lamp was placed ten centimeters from the bottom of the tube. None of the animals left the bottom in seven minutes of continuous observation. The tube was inverted then (so that all the animals were in the top section) and the 15-watt at the top of the tube was turned on at 1:56 P.M. At 2:00 P.M. the distribution was 2, 1, 1, 0, 4; at 2:03 P.M., 2, 0, 2, 1, 3; at 2:07 P.M., 1, 0, 1, 1, 5 at 2:10 P.M., 1, 0, 0, 0, 7. Here the light was cut off, and at the end of ten minutes in darkness the distribution was still 1, 0, 0, 0, 7. Evidently the animals did not ascend in darkness. Then at 2:21 P.M. the tube was inverted again, putting seven animals in the top and one in the bottom section and darkness was continued. At 2:25 P.M. the distribution was 0, 0, 2, 3, 3; at 2:28 P.M., 0, 0, 0, 0, 7; at 2:43 P.M., 0, 0, 0, 0, 7; at 3:00 P.M., 1, 0, 0, 1, 6; at 3:20 P.M., 2, 1, 2, 0, 3; at 3:45 P.M., 2, 0, 1, 0, 5; at 4:00 P.M., 2, 0, 0, 0, 6; at 5:25 P.M., 5, ?, ?, ?, 2; at 8:00 P.M., 6, ?, ?, ?, 1.

While these details are intended chiefly to show the positive geotropism of deep water animals, they incidentally reveal negative phototropism, and the onset of negative geotropism about 6:00 P.M. This latter point has been dealt with in another place (Esterly, 1917*b*, p. 396, table 3). There is no reason to doubt that the behavior shown by the animals from deep water is characteristic of the species, but the data might well be more extensive.

In contrast to the behavior of the deep-water specimens animals from the surface are negatively geotropic in the diffuse light of a room and positive in darkness. Since one could not depend upon getting surface animals except at night it was necessary to leave the experimental specimens in the laboratory for a few hours at least. A few preliminary tests indicated that individuals from the surface react at once as they do after six or eight hours, and I have assumed, therefore, that retention in the laboratory does not affect the behavior of animals

that were obtained at the surface during the night. Table 1 (p. 20) is a summary of the distribution of four different sets of animals (A–D) in a column of water. The tube containing the animals was marked off into five equal divisions and exposed to light for a short time and the distribution noted one or more times. Then it was covered so as to exclude all light, and after an interval the cover was removed and the distribution noted. The alternation of light and darkness was repeated several times, and all the records for a given set of animals are put together in the four lines of each half of the table.

The form of tabulation used in table 1 is found in others in this paper, and the following explanations of terms will apply to all tables of this sort. The "whole number of animals observed" is the sum of all records of distribution in all experiments. Each living animal was counted as many times as there were observations made: if there were five individuals in a tube and their distribution was recorded ten times, the "whole number observed" would be fifty. If it is necessary to count quickly it sometimes happens that all the individuals known to be in the container can not be located; in such cases the "whole number" does not equal the product of "number of individuals" by "number of observations." "Percentage distribution in the sections" is the proportion of the total number of animals observed *in each section,* to the whole number observed. "Number of observations" means the number of times the distribution was recorded. The "center of distribution" is the average position (as between the ends of the container) of the whole number of animals observed. It is obtained by multiplying the total number of animals recorded in each section by the number of the section, and dividing the sum of the products by the "whole number of animals observed." The centers are set down in units and tenths and the unit is considered as the middle point of the section having the corresponding roman numeral. If one center is compared with another the difference between them, if any, is the magnitude of the shift of the whole population. This useful method of expressing average position was first used, so far as I know, by Yerkes (1899).

The ascent is accomplished by means of swimming while in descending the animals drop passively, with the head uppermost and the anterior antennae spread to their full extent. The passive descent continues after the animals are lighted, following a short time in darkness, but in a few seconds they begin to swim up in characteristic jerky fashion.

TABLE 1

Summary of the Vertical Distribution of Different Sets of *Acartia tonsa* from the Surface for Alternating Periods in Diffuse Light and in Darkness; all Records for each Condition and for each Set are Combined. Temperature Above 17° C; Salinity not over 34 $^0/_{00}$.

Set	Whole number of animals observed	Percentage distribution in the sections (top V)	IV	III	II	bottom I	Number of observations: Total	per cent showing more animals in: upper %	lower %	Center of distribution
					In the Light					
A	68	53	33	8	4	2	4	100	0	4.1
B	221	55	21	13	4	7	11	100	0	4.1
C	184	51	24	7	2	16	9	100	0	3.9
D	99	57	18	9	8	8	5	100	0	4.1
					In the Dark					
A	46	13	19	9	9	50	3	33	66	2.4
B	227	15	12	23	4	46	10	40	60	2.4
C	180	12	11	7	5	65	9	0	100	1.9
D	94	23	9	3	7	58	5	40	60	2.3

The evidence given in the table shows clearly the marked negative geotropism in diffuse light and the positive geotropism in darkness. It may be pointed out that most of the animals were in the upper two-fifths every time the distribution was recorded when the animals were in the light. The percentage distribution and the centers of distribution also show that there is a well-marked ascent in the light and descent in the dark.

In connection with the geotropism of surface animals it is suggestive to note that on the only occasion when I tested animals that were obtained at the surface during the day they were positively geotropic in diffuse light. The phototropism was not ascertained. These animals were obtained at 7 A.M., but were not used until 1 P.M. The majority swam to the bottom and that general distribution was not altered up to 4 P.M. when observation ended. Such observations are not of much value unless followed up, but they seem to fit in with those regarding the geotropism of subsurface animals. It almost seems that the physiological condition that leads to the descent was present in those particular surface animals even though they were obtained at the surface, and that the same state persisted for several hours. The difficulty about extending such observations is in obtaining animals from the surface during daylight.

I have made a few observations on the behavior of single animals from the surface when the 15-watt lamp is directly above or below the

tube. The animals are very hard to see under these conditions, but I believe that the small amount of data that I have to report really shows the behavior of the species. The account that follows is a summary of the results obtained with eight individuals. I recorded the position of each animal at intervals, noting whether the movement was up or down, and a record was kept also of the distance covered in each direction. It is possible, therefore, to state, first, what proportion of the animals moved up or down; second, the relative proportion of recorded changes of position in either direction; and third, the percentage borne by the distance traversed either up or down to the entire distance covered. There is more or less movement in both directions under either condition of lighting; but, as the figures will show, the direction of movement depends chiefly on the position of the light. *With the light at the top of the tube,* 80% of the records show movement toward the top and 20% show the reverse; and in a total of 380 centimeters traveled, 93% of the distance was toward the light (that is, negative geotropism) and 7% was away from the light (that is, positive geotropism). *With the light at the bottom of the tube,* 19% of the records show movement toward the top and 81% show the reverse; and in a total of 491 centimeters traveled, 91% of the distance was toward the light (that is, positive geotropism) and 9% was away from the light (that is, negative geotropism). It need not be said that the animals *swim* up, if they move in that direction at all, but they also swim down when the light is at the bottom. The downward movement is actively brought about instead of being a passive descent.

SUMMARY

The following facts about the behavior of *Acartia tonsa* and *A. clausi* seem to be adequately established: (1) Surface animals are positive to light of any intensity in water above 16° C. (2) At lower temperatures there is a tendency to negative phototropism, especially in *clausi* (Esterly, 1917*a*). (3) Animals from deep water show a strongly marked negative phototropism which disappears if they are kept in the laboratory (Esterly, 1917*a*). (4) Surface animals are negatively geotropic in diffuse light, and in darkness they are positive. (5) Specimens from deep water are positive in geotropism both in diffuse light and in darkness if tested soon after they are removed from the ocean. (6) Both species show a rhythm in geotropism which does not appear to be connected with external changes acting at the time (Esterly, 1917*b*).

POSSIBLE BEARING OF THE EXPERIMENTS ON DIURNAL MIGRATION

If only specimens from the surface were at hand the experiments would lead us to conclude that the animals are more abundant at the surface during the day and less abundant at night. While figures based on field data are not yet available it is certain that this sort of distribution is unusual. Specimens of *Acartia tonsa* from deep water react as one would expect of animals that forsake the surface during the day: they are positively geotropic in the light and negatively phototropic; but they are also positively geotropic *in darkness* until late afternoon or early evening, when there is an upward scattering. This latter fact, coupled with the rhythmic behavior of surface animals that are kept in darkness for hours, very strongly suggests that the ascent will take place in the absence of external stimuli. It is possible that the animals descend when the physiological state that led to the upward movement wears off. At any rate the experiments do not show why animals obtained at the surface should not be found there during the day; indeed the laboratory results show that the species "ought" to be at the surface during the day. The experiments furthermore suggest that during the colder months of the year more animals will be found at the surface than during the summer, since in colder water there is an increase in the number of animals in the upper parts of a column of water (Esterly, 1917*b*, p. 395, table 2).

Reactions of the Copepod *Calanus finmarchicus*

More attention was given to the reactions of this form than of any other because it was readily obtained and because it is the most abundant copepod in the field collections that have been studied. *Calanus* is from three to four millimeters in length and the body is somewhat opaque so that it is not as hard to see as some of the copepods. The animals are hardy and withstand laboratory conditions well, but for reasons already given I made it a general practice to use only fresh specimens. All the animals that were used in experiments were obtained at sixty to one hundred meters by lowering the net and allowing the boat to drift. None were obtained from the pier either by day or night. Several unsuccessful attempts were made to get animals from the surface at night by towing from a boat well offshore.

PHOTOTROPISM

When specimens are brought from such depths to the surface in a short time there is an abrupt change in environment of considerable extent. It is hard to say what effect this has on the responses observed in the laboratory. It is suggestive, however, that when the catch is first brought in and put into a dish before the window most of the animals are positive to the light. Individuals, also, when tested alone swim toward the light. In the stock dish the animals dart around continually; some even swim across the dish to the room side but immediately return to the side next the window. At any time, however, shortly after the animals are received there is a marked assemblage as near the window as possible. But this condition gradually disappears. More and more animals are found on the room side of the dish until all or nearly all are gathered there. It is not unusual to find one or two animals that are persistently positive, while others may swim from the negative to the positive side and back again. Such trips in either direction are straight across the dish; the animals do not wander about.

An example of the behavior of six animals in a dish 21 cm. in diameter will serve to illustrate what has just been said. They were brought to the surface from sixty meters at 9:15 A.M. and observations were begun at 9:40 A.M. The dish was marked off into five divisions parallel to the plane of the window and of equal width along the diameter perpendicular to the window. The number of animals in each division was noted at brief intervals, and the results are summarized in table 2 (p. 24).

Inspection of the table shows that there is a gradual increase in the number of animals in sections IV and V and a gradual decrease in numbers in I and II, while the center of distribution shifts from the window to the room side of the dish. The length of time varies a good deal within which the different sets of animals become predominantly negative. But when the animals are tested after they have been in the laboratory for some time they are very strongly negative to light.

If several animals are put into a dish which is turned end for end toward the window they swim from the end nearer the window to the one opposite, time after time, as the ends are reversed. In table 3 (p. 24) there are summarized the results of testing two different sets of animals in this way. Some records which enter into

the table were obtained on the fourth day after the animals were brought in, so that the table is not intended to show more than the strong negative reaction of the copepods. The animals were released in the center of the dish one by one, and in a few minutes the vessel was turned through 180° and the distribution noted at short intervals. The turning was repeated several times, and table 3 contains the summary of the results.

TABLE 2

The Changing Distribution of Six Specimens of *Calanus* in a Dish of Water Standing Before the Window. The Animals were Brought in at 9:15 A.M. and were kept in the Water that was in the Collecting Jar, at Temperature of about 16°C.

Time A.M.	Whole Number of animals observed	Percentage distribution in the sections: Negative V	IV	III	II	Positive I	Number of observations: Total	per cent showing more animals in: positive %	negative %	Center of distribution
9:40– 9:44	18	39	....	5	....	56	3	33	33	2.7
9:50– 9:55	18	11	33	17	....	39	3	33	33	2.2
9:57– 5:59	18	39	....	5	....	56	3	66	0	2.7
10:00–10:04	30	43	3	7	7	40	5	40	40	3.0
10:05–10:09	30	47	7	3	13	30	5	0	0	3.3
10:10–10:14	30	63	3	3	7	24	5	0	100	3.8
10:15–10:19	30	56	20	7	7	10	5	0	100	3.8
10:20–10:24	30	66	7	7	....	20	5	0	100	3.5
10:25–10:29	30	63	0	7	7	23	5	0	100	3.7
10:30–11:00	108	77	1	4	5	13	18	0	100	4.2
11:25 A.M.– 1:50 P.M.	30	93	0	0	3.5	3.5	5	0	100	4.8

TABLE 3

Distribution of Specimens of *Calanus* in a Dish 20 by 8 cm., Divided into Five Equal Sections. The Dish was Turned at Intervals so that the Ends Came Alternately Next the Window. Temperatures Above 17° C; Salinity not over 34 ‰.

Whole Number of animals observed	Percentage distribution in the sections: Negative V	IV	III	II	Positive I	Number of observations: Total	per cent showing more animals in: positive %	negative %	Center of distribution
946	59	9	10	5	17	138	5	95	4.

Since the intervals between observations were short some animals were recorded as in sections nearer the window when, as a matter of fact, they were really moving away from the light. Some, indeed, did not move out of a given end section at all, whether it was next the window or not. But on the whole the table shows the strong negative phototropism of *Calanus*.

Much of the testing was done with individual specimens. I followed the plan of making frequent records of the distance and direction traveled by each animal under observation. Each time that the position was noted, the distance and direction of any movement and the time elapsed since the last record was set down. While the rate of movement is relatively unimportant for our purposes, distance and direction indicate precisely the kind of response. Response means *position* at a given moment as compared with that at the previous time of observation. If it is decided to note the position every fifteen seconds, for example, each record that shows change of position surely denotes a response as compared with a preceding record. Of course an animal may be watched until it has traveled as far as the limits of its confinement will allow and that may be recorded as one reaction. But noting often will indicate whether an animal moves back and forth or not; whether its progress is continually away from the light, for example. Some records of position that do *not* show change of position on the part of the animals indicate, nevertheless, that there is a response and the nature of it. My plan has been to regard each record of position set down in my notes as showing the kind of reaction. The terms "observation," "response," "reaction" and "record of position" are practically the same.

In explanation of table 4 and others like it that follow, it needs to be said that the columns headed "records of position" show the number of times that the location was set down. If the specimen moved during the interval between two records (up or down, or toward the light, or away from it) the change of position is in the nature of a reaction. But it often happens that there has been no change in position from one observation to the next; this is also noted under "records of position." It may at once be asked, What is the use of entering a record that does not show movement on the part of the animals? One reason is that it seems desirable to present all the data in order to show as fully as possible just what the behavior is. A second reason is that "no movement" or "no change of position" may mean just as much in the way of reaction as actual locomotion. For instance, when an animal ascends in a vertical tube as far as it can and constantly maintains that position, successive records would show that there has been no upward or downward movement. But the fact that the specimen remains at the top is as good evidence that it is negatively geotropic as the fact that it swims to the top in the first place. Similarly, an individual may descend to the bottom

and remain there. The "records of position" obtained during the descent are entered as those that show movement. But if after the bottom is reached the animal remains there it is good additional evidence that it is positively geotropic. It is possible, of course, that an animal which remains at the bottom may be too fatigued to ascend although it is really negatively geotropic. I believe, however, that sufficient precautions were taken in these experiments to guard against such occurrences. The plus and minus signs at the top of the "no movement" columns refer to the *direction of the last recorded movement*. If the animal is in a vertical tube the plus sign in the "no movement" column means that after a descent of greater or less extent there had been no movement upward at the time the next record was put down. Likewise, the minus sign indicates that following a movement upward there was no descent. There is nothing in the summary in the tables to show at what level the animals remained stationary; but, as a matter of fact, most records that show no vertical movement are for animals on the bottom of the container or at the top of the column of water. Some records of position that show no movement were obtained because of what appears to be a thigmotactic reaction against the walls of the aquarium; at such times the animal is stationary. But these records are not numerous enough to change the general results.

As regards the "per cent of animals moving" (table 4, for example) it doubtless will be perplexing to the reader to note that the sum of the two percentages under the heading may exceed 100. In explanation it may be said if an animal moved at all toward the negative end that fact was noted, and if there was any movement toward the positive end that also was set down. It does not matter how many *times* or *how far* an individual is recorded as moving in one direction or the other; if the animal changed position once or a hundred times the tally would show 1 in either case, so far as "per cent of animals moving" is concerned. For example, it is possible that one individual in a set of five may be recorded as having changed position once toward the positive end and twenty times toward the negative end; but that particular specimen would count as one animal in the negative column and one in the positive column. The other four may all have moved toward the negative end only, and in the summary of the behavior of the set the figures would be: positive 20%, negative 100%. This example is not an actual one, but it ought to show why it is that such results appear as those in the fifth and sixth columns of table 4. The same explanation holds for other tables of the form of table 4.

It is worth noting that in the tables dealing with the summary of individual performances there are three items that indicate the kind of response and the relative degree to which it is manifested: (1) The relative number (expressed as percentages of the whole number of animals) of individuals that move in the positive and negative direction. These numbers may be about equal, but either or both of the following items will show more adequately the actual extent of positiveness or negativeness. (2) The proportion between the records that show positive and those that show negative changes in position. For instance, if an individual is recorded as moving toward the bottom three times out of four and toward the top once it is good evidence that it is a positively geotropic animal. (3) The distance traveled in either direction is a very satisfactory index of the degree to which one kind of reaction exceeds the other. If the figures giving the number of animals moving and those giving number of records should be about the same in the positive and negative columns, while the figures that show distance covered are very unequal (as between positive and negative), I should be inclined to hold that the latter reveal the kind of response given under the particular conditions of the experiment.

The differences between the figures in the positive and negative columns for each of the three items should always be compared when considering the tabulated results. When the differences point in the same direction in all three cases, the evidence is a good deal stronger than if one difference indicates one thing and a second shows something else.

It is desirable to note, in further explanation of the use of terms, that "number of experiments" means the total number of times it was attempted to ascertain the behavior of individuals under a given set of conditions. The average number of trials given each animal appears from the ratio between number of experiments and number of animals tested.

The table that follows (p. 29) contains the summary of the records of individuals. The behavior under all intensities of light is included in the summary, since the phototropism does not change with the intensity as it does with the temperature. The extreme ranges of intensity employed (as compared with the 15-watt lamp) were from 0.025 to 15,000 or more, with such intermediate intensities as 8, 196, 3800.

The figures in the first line show that *Calanus* is strongly negative to light. The range in temperature is that of the room at different seasons of the year, and the salinity is that of sea water as it came

from the pipes or from the ocean directly. It is possible to account for some of the positive responses. When an animal is enclosed in a tube that is horizontal with one end toward a light it may swim to the negative end and from there make short dashes toward the light and back again to the end. The method of recording that I used makes it possible to take note of such positive movements. I do not believe that such behavior is due to positive phototropism. It is rather due to the incessant activity, and after an animal has reached the end of a tube it can only swim toward the light. Some cases, however, are due to what seems to be a positive response, as such. If the animals are tested soon enough after they come into the laboratory they are, as already stated, usually positive, and some records of such animals enter into the table. It has occasionally happened that an animal after having gone from the light several times suddenly reversed and traveled toward the light a few times and then returned to the former kind of response. These records also are part of the first line in table 4. But in general laboratory animals are strongly negative to all intensities at ordinary temperatures and concentrations of the water.

If the results in the third line are compared with those appearing in the first it will be seen that the differences in the percentages are in favor of the positive instead of the negative side. That is, the animals become positively phototropic in water of low temperature. It was outside my purpose to try to ascertain the point at which there appears a well defined positive reaction when the temperature is gradually decreasing, or a negative reaction when the temperature increases slowly. But table 5 (p. 30) will give the results of observing the behavior of six animals in a dish while the temperature fell gradually and then slowly rose. As usual, the dish was divided into five sections, section I next to the light and section V opposite. In water as cold as 6° C the animals swim around as freely and actively as at 15° C.

The table does not need further explanation. It shows the gradual change from negative to positive as the temperature slowly decreases and the reverse when it increases from the low points. Individuals are continually swimming back and forth, and this accounts for most of the animals noted in sections other than the one next the light, or it is turned through 180° while the position of the light is not changed. Or they will swim back and forth across the vessel when a 15-watt lamp on one side is alternated with a 100-watt on the other, the movement being toward the illuminated side of the aquarium.

TABLE 4

THE PHOTOTROPISM OF *Calanus* UNDER DIFFERENT CONDITIONS OF TEMPERATURE AND SALINITY.
SUMMARY OF INDIVIDUAL RECORDS

Temperature	Salinity ‰	Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
							per cent of total showing					Per cent	
							movement		no movement		Total (cms.)		
				+	—	Total	+	—	+	—		+	—
14°–20°C	33–34	386	65	52	88	1,167	20	56	10	14	7,006	21	79
14°–20°C	37–40	116	50	62	90	543	32	50	9	9	2,979	25	75
6°–9°C	33–34	83	17	74	24	100	82	18	0	0	728	80	20
6°–9°C	37–40	37	16	75	81	255	40	17	33	10	548	60	40

On the whole, the fact that the animals become positive in water of low temperature is clear and unmistakable.

If the salinity is increased while the temperature remains that of the room (second line of table 4) there is no significant change in the behavior as compared with that at ordinary temperature and salinity (line 1). The animals are clearly negative to light under both conditions, and it does not appear that there is positive phototropism to an increased extent when the concentration of the water increases. As a matter of fact it is shown in line 4 that at high salinities and low

TABLE 5

The Changing Distribution of Six Specimens of *Calanus* in a Dish Divided into Five Sectons, as the Temperature Decreased Slowly and then Increased Salinity 33 to 34 $^0/_{00}$.

Temperature (°C)	Time p.m.	Number of animals in the sections: negative V	IV	III	II	positive I	Number of observations	Center of distribution
16	1:50	6	0	0	0	0	1	5
13⅜	2:10	1	0	0	2	3	1	2
11⅜	2:20	2	1	0	0	3	1	2.8
10	2:25	0	1	1	0	4	1	1.8
8⅛	2:35	1	0	0	1	4	4	1.8
6–7	3:20–4:00	4	0	1	0	19	4	1.7
5⅛–8⅜	4:14–5:21	10	2	12	4	138	27	1.4
8⅜	5:35–5:37	0	0	0	0	12	2	1
9⅜–9⅛	5:40–5:43	1	1	0	1	15	3	1.4
10⅛–10⅜	5:45–5:47	2	2	1	0	13	3	1.9
10⅛–11⅜	5:50–5:55	10	1	1	0	13	5	2.3
13⅛–14	6:30–6:34	19	0	2	0	9	5	3.7
14–14⅜	6:35–6:40	18	0	0	1	17	6	3.7

Note.—From 1:50 to 2:35 the animals were exposed to the light from three north windows; for the rest of the time to the light from the 100-watt lamp without the "daylite" filter through an opening 10 cm. square, the center of the coil being 14 cm. from the wall of the aquarium; this intensity is about 200 times that of the 15-watt lamp.

temperatures there is less positive and more negative phototropism than when the temperature is low and the salinity normal. It is difficult to say, however, how much significance there is in the results given in the last line of table 4, but it would seem that the high salinity counteracts to some extent the effect of the low temperatures. Loeb (1893, p. 98) states that increase of concentration increases the positivity of copepods and also of *Polygordius larvae* (p. 94). Ewald obtained similar results with *Balanus larvae* (1912, p. 606). It is certain that *Calanus* does not become increasingly positive in water of high salinity.

Conclusions. *Calanus* is negative to light of all intensities except when the water is cooled. The phototropism becomes noticeably positive at about 13° C, and is pronouncedly so at temperatures below 10° C. There is no marked change in reaction when the salinity is increased if the temperature is not lowered; the phototropism is negative. But there is some indication that the positivity decreases, relatively, in water of low temperature and high salinity.

GEOTROPISM

In sea water of ordinary temperature and salinity *Calanus* is always positively geotropic except when lighted from below. The animals descend to the bottom and remain there except for what may be called accidental dashes upward. If put into a column of water the specimens do not swim down, under ordinary conditions, but they drop down passively. The descent is sometimes interrupted by swimming to the side of the tube where the animal may cling for a short time or bump against the glass, but it soon begins to drop again. An animal may even make a short ascent, then drop, then ascend, and so on, each upward movement being of less extent than one in the opposite direction so that the individual gets lower and lower in the tube. When dropping passively the long axis of the body is not quite perpendicular but the anterior end of the animal is always uppermost. The axis is inclined toward the dorsal side about 25° from the perpendicular, and the anterior antennae are always extended at right angles to the body. Under certain conditions *Calanus* will *swim* down, head foremost, with the axis of the body at an angle of 45° to 90°. The dorsal surface is uppermost in swimming down unless the body is perpendicular.

It is necessary to state that in the experiments on geotropism a temperature or salinity gradient was used as well as uniform conditions of both these factors. The lower two-fifths of a tube containing ordinary sea water was set into ice water, or this was done when the water in the tube was of high salinity, or the entire container was chilled when it held water of normal or of high salinity. And in some cases the tube held water of high salinity in the lower part and normal sea water in the upper part, with the lower two-fifths of the tube surrounded by ice. There is no evidence from my results that the behavior in a gradient differs from that shown when the water in the tube is of the same temperature or salinity in all parts. In tabulating

the results, therefore, no distinction is made between gradients and uniform conditions.

In diffuse light (table 6). When the lighting conditions are those of a room, or when the light comes from one side only, as in the dark room with the window open or with a lamp at one side, the geotropism of *Calanus* is almost uniformly positive. The figures given in table 6 offer abundant evidence of this. So far as the experiments go, the geotropism does not change with alterations in temperature or salinity (Cf. lines 1 and 3, and 1 and 2). The animals descend and remain at the bottom under all conditions. If the water in the tube offers a salinity and temperature gradient the animals drop into and down through the cold and highly concentrated strata without any change in behavior and remain at the bottom.

The general results in table 6 are so consistent that further comment is unnecessary.

In darkness (table 7). The prevailing positive geotropism in darkness is shown by the figures in the table. The animals descend to the bottom and remain there. The behavior in darkness was ascertained by momentarily lighting the aquarium to discover whether there had been a change in the position of the animal. When the light is flashed on, the animals are passive for a moment, then dash wildly about for two or three seconds and then suddenly become quiet; if they happen to have darted upwards they drop to the bottom as can be seen if the light remains on. There is no doubt, however, that if started at the top the animals descend and when once at the bottom they do not move up. If the time of illumination for the observation after a period in darkness is short enough the animal continues to drop without any other movement, and the presumption is that the same mode of progress is in operation in the dark. There are no significant changes of behavior when the temperature is lowered or when the salinity is increased. It may be well to explain, however, that in the third line of the table the large percentage of "no movement" records in the positive column is due to the fact that the time was prolonged after the bottom was reached in order to see if the animals would ascend in the cooled water. The result is that more records than usual were entered in my notes while the animals were on the bottom.

In vertical light from above (table 8, p. 35). All the experiments were performed with the 15-watt lamp directly above and ten or twenty centimeters from the surface of the water in a tall museum jar,

TABLE 6

THE GEOTROPISM OF *Calanus* IN DIFFUSE LIGHT UNDER DIFFERENT CONDITIONS OF TEMPERATURE AND SALINITY.

SUMMARY OF INDIVIDUAL RECORDS. TUBE 50 CM. LONG, 3 CM. WIDE.

Temperature	Salinity ‰	Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
							per cent of total showing						
							movement		no movement			Per cent	
				+	—	Total	+	—	+	—	Total (cms.)	+	—
14°–20°C	33–34	201	32	72	12	580	70	2	26	2	6,498	99+	.06
14°–20°C	37–40	34	20	100	0	192	85	0	15	0	1,131	100	0
8°–11°C	33–34	5	5	60	0	36	47	0	53	0	135	100	0
8°–11°C	37–40	0	0	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

TABLE 7

THE GEOTROPISM OF *Calanus* IN DARKNESS UNDER DIFFERENT CONDITIONS OF TEMPERATURE AND SALINITY.

SUMMARY OF INDIVIDUAL RECORDS. TUBE 50 CM. LONG, 3 CM. WIDE.

Temperature	Salinity ‰	Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
							per cent of total showing						
							movement		no movement			Per cent	
				+	—	Total	+	—	+	—	Total (cms.)	+	—
14°–20°C	33–34	109	42	95	7	385	78	4	17	1	4,302	98	2
14°–20°C	37–40	43	27	100	0	153	92	0	8	0	1,680	100	0
8°–11°C	33–34	21	15	66	20	103	42	6	41	11	470	93	7
8°–11°C	37–40	18	9	60	12	74	89	4	4	3	557	99	1

or more often a tube 50 by 3 centimeters. The animals are very strongly positive at room temperatures (lines 1 and 2), and this behavior is not altered by changing the salinity. In a good many instances the specimens swim down for at least a portion of the distance and swimming often alternates with dropping.

A comparison of the figures indicating movement in the first two lines with the last two shows that at the lower temperatures there is a considerable decrease in the percentages in the positive column and an increase in the negative column. In other words, the animals move toward the light more often when the temperature is low even if it involves overcoming gravitation. Such a change in behavior is not shown in tables 6 and 7, so it is to be presumed that the upward movement shown in table 8 is a reaction to light rather than to gravity. That is, the animals become positive to a vertical light as well as to a horizontal one, providing the water is of a sufficiently low temperature. It is interesting to note that when the lower two-fifths of the column is in ice water in some cases the animals do not ascend farther than the level of the cold water on the outside of the glass. On the other hand, some individuals, under similar conditions, will swim upward through the remaining three-fifths of the column (although that part is at room temperature) and will remain at the top for a short time. But even when the entire container is immersed in ice water the animals do not remain long at the upper levels, but gradually get farther and farther away from the surface. A number of short ascents may be made, but after each ascent the animal drops back a greater distance than it swims upward, so that finally it reaches the bottom.

It is evident, on the whole, that under the lighting conditions given in table 8 there is a certain amount of reversal of geotropism from positive to negative at the low temperatures. When the water is cooled and is also of high salinity (line 4), the behavior is substantially the same as in cooled water of the usual degree of salinity (line 3).

In vertical light from below (table 9). This experimental setting does not apply to natural conditions but it is helpful for interpreting behavior. In these tests the 15-watt lamp was used, and it was always about fifteen centimeters from the center of the bulb to the bottom of the aquarium. The containers were either museum cylinders, 35 by 6 centimeters, or tubes, 50 by 3 centimeters.

As is shown in the first line of table 9 there is more movement up than down at the usual temperatures and salinity. This is especially evident if line 1 is compared with the first lines of tables 6, 7

TABLE 8

THE GEOTROPISM OF *Calanus* IN VERTICAL LIGHT FROM ABOVE AND UNDER DIFFERENT CONDITIONS OF TEMPERATURE AND SALINITY. SUMMARY OF INDIVIDUAL RECORDS

Temperature	Salinity ‰	Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
							per cent of total showing						
							movement		no movement			Per cent	
				+	—	Total	+	—	+	—	Total (cms.)	+	—
14°–20°C	33–34	81	40	97	1	229	88	1	11	0	3,689	99	1
14°–20°C	37–40	38	27	100	4	169	87	3	10	0	1,552	99	1
8°–11°C	33–34	22	16	56	75	452	22	22	47	9	626	53	47
8°–11°C	37–40	26	16	69	25	322	17	15	66	2	452	61	39

TABLE 9

THE GEOTROPISM OF *Calanus* IN VERTICAL LIGHT FROM BELOW AND UNDER DIFFERENT CONDITIONS OF TEMPERATURE AND SALINITY. SUMMARY OF INDIVIDUAL RECORDS

Temperature	Salinity ‰	Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
							per cent of total showing						
							movement		no movement			Per cent	
				+	—	Total	+	—	+	—	Total (cms.)	+	—
14°–20°C	33–34	120	49	70	61	1,007	19	27	40	14	4,574	44	56
14°–20°C	37–40	48	27	81	81	398	25	47	22	4	2,022	14	86
8°–11°C	33–34	26	15	66	33	468	17	13	63	7	855	57	43
8°–11°C	37–40	30	16	81	31	241	27	14	59	0	654	74	26

and 8. When lighted from beneath many animals swim rapidly away from the light, but there is a good deal of difference in individuals. Some, apparently those that have been too long in the laboratory, do not leave the bottom at all, or, if they do ascend, move only a few centimeters. But animals that have been freshly brought in are very consistent in their behavior; they all leave the bottom and remain at or near the top for hours.

In order to show how pronounced the negative geotropism is when the light enters the tube from below an experiment may be cited in which six animals were put into a jar 35 by 6 centimeters (marked off into five sections) an hour after they were brought to the surface in the net. The light at the bottom was turned on at 10:44 A.M. and at 10:47 all were in the top section. From that time until 4:05 P.M., 98 observations were made; not an individual was observed in the bottom section; two were seen in the second from the bottom, six in the middle section, twenty in the second from the top, while 560 (about 94 per cent) were recorded in the upper section. Some animals are always dropping down from the top; they descend in that way for a longer or shorter distance and then swim back to the top. I have not looked closely into the reason for the persistence with which some animals, as shown in table 9, stay at the bottom, but it appears to be connected with some effect due to laboratory conditions.

When the temperature at the bottom of the column of water is low, there is an increase in positive geotropism; the animals stay more persistently at the bottom. This is probably a positive response to the light, but the whole effect is that of positive geotropism. If the whole column of water is chilled it can be noted that there is a tendency for animals that are started at the top to swim down. If, however, the upper part of the water in the jar is at room temperature while the lower portion is surrounded by ice the animals descend more slowly or even keep ascending time after time, but sooner or later they reach the cold water near the bottom. Then the tendency to ascend largely disappears. The most striking feature of the behavior when the aquarium is lighted from below and the lower part of it is in ice water is the failure of the animals to leave the bottom; but it is also evident that downward movement is increased and upward decreased when the animals encounter colder water. When the salinity is increased (line 2) while the temperature is that of the room, the negative geotropism is increased. But the positive geotropism is increased if the salinity is raised and the temperature lowered (line 4),

so that the behavior in cooled water of high salinity is about the same as in water of low temperature and normal salinity.

Physiological rhythm in geotropism. Will *Calanus* ascend in a column of water if there is no apparent change in external conditions that can direct the movement? It has been shown that the animals descend in diffuse light as well as in darkness under all conditions of temperature and salinity in the laboratory. They do not ascend during the day from 8 A.M. to 4 or 5 P.M. under experimental conditions except when driven up by light beneath or except for the continual and incidental movement already described. But I have found that under certain circumstances there is more or less of a general upward movement even when directive stimuli are absent.

On one occasion fifteen animals that had just come in were put into a cylinder 35 by 6 centimeters marked off into five equal divisions. The lower two-fifths of the cylinder were immersed in ice water and kept at 8°–10° C throughout the experiment, while the water in the remainder of the cylinder was from 16°–17° C. During the day the experiment was carried on in the dark room in daylight of an intensity amounting to about 1.2 as compared with the 15-watt Mazda. When night came on observations were taken in artificial light that was used for as few seconds as possible and then extinguished, the animals being in darkness for the rest of the time. The upper half of table 10 shows how the animals were distributed during the day and the early part of the night.

TABLE 10

THE DISTRIBUTION OF *Calanus* IN A COLUMN OF WATER, THE LOWER PART OF WHICH WAS 5°–10°C THE TOP 16°–18°C. TWO DIFFERENT EXPERIMENTS IN THE TWO HALVES OF THE TABLE. SALINITY 33 TO 34 ‰.

Time	Whole number of animals observed	Number of observations	Percentage distribution in the sections: top V	IV	III	II	bottom I	Center of distribution
1:00–7:00 P.M.	195	13	0	0	0	0	100	1.0
7:20–10:00 P.M.	195	13	10	3	4	11	72	1.5
10:30 A.M.–5:20 P.M.	610	61	0	0.1	2	7	91–	1.1
6:45 P.M.–10:30 P.M.	90	9	21	9	16	21	33	2.6

A second experiment of this kind was conducted with fresh material. Ten animals were put into a cylinder 35 by 6 cm. and the lower two-fifths of it was surrounded by ice; the temperature in those sections did not rise above 8½° C and it was as low as 5° C, while the temperature in the three upper sections was from 17°–18° C. The

distribution of the animals is summarized in the lower half of table 10. During the day they were in very dim diffuse light in the dark room; after dark the observations were made in the light of the 15-watt lamp. During this second experiment another cylinder was set up, identical with the other one and containing control animals from the same collection. But the temperature was about 18° C throughout the length of the control cylinder; otherwise the conditions were the same in both. The distribution in the control may be dismissed by saying that from 10:30 A.M. to 8:50 P.M. fifty-five observations were recorded. On two occasions one animal was noted in the second section from the bottom, but all the others were in the lower section throughout the experiment.

The results set forth in table 10 are more striking in the case of the second experiment, especially when the behavior of the control animals is considered. I believe that these experiments, in spite of the somewhat meager results, indicate the existence of a factor that must be taken account of in connection with diurnal migration. The fact that the upward movement in the laboratory does not take place except when the animals have been in cold water is significant in view of the temperature distribution in the sea. Table 10 shows that but a small part of the animals moved upward, but I believe that this can be accounted for in part at least. When the light is turned for observation after nightfall, the animals do not move at once; the quiescent period is long enough for one to note the distribution accurately. But even when the observation is made quickly there is more or less dashing around. Some dart down and others up, so that the distribution is upset every time an observation is taken. These unavoidable complications probably make the upward movement appear less extensive than it really is.

There is evidence, therefore, of a physiological rhythm in *Calanus* as in *Acartia*. The animals ascend at a particular time of the twenty-four hours but not during the period of daylight.

SUMMARY

(1) The phototropism of *Calanus* is predominantly negative at ordinary temperatures, but it becomes markedly positive in water of 10° C and less. The reactions to light do not change when the salinity is increased. (2) The geotropism is very strongly positive in diffuse light and in darkness, and the behavior does not change with changes in temperature and salinity. (3) When the light falls vertically from

above the vertical movements of the animals are practically all downward except in water of low temperatures. There is then a comparatively marked tendency to ascend. There is no marked change in behavior with change in salinity. (4) When the animals are lighted from below there is marked movement upward at ordinary temperatures, and this increases in water of high salinity. The amount of movement away from the bottom decreases at low temperatures, especially as regards the distance covered. The animals remain at the bottom more persistently when the water in the lower part of the column is chilled than when it is at room temperature. (5) Animals in weak, diffuse daylight do not show any tendency to ascend. But after nightfall a noticeable upward migration begins to appear in a column of water whose lower portion has been cooled to 8° C or 9° C, although no change that might affect the direction of movement has taken place in the surroundings. Some of the animals swim into water eight or nine degrees warmer than that in which they started. This behavior is not shown in a cylinder where the temperature throughout is 16°–18° C.

POSSIBLE BEARING OF THE EXPERIMENTS ON DIURNAL MIGRATION

The general facts of the distribution of *Calanus* in the ocean are well established by our field work. The animals are less abundant at the surface by day and more abundant in deeper water; at night they are less abundant in deeper water and more abundant at the surface. It is assumed that upward migration leads to the increase in numbers at the surface, and that downward migration leads to the greater numbers in deeper water. How can the results of experiments be applied to explain this general condition? Since the copepods are strongly negative to light at temperatures of 14°–20° C, that fact would explain their absence from the surface of the sea during the day, assuming that the reactions to vertical and horizontal light is the same. Furthermore, since the phototropism becomes positive at lower temperatures we might expect that the animals would begin to move toward the surface of the sea if, in the course of their descent, they reach water of a sufficiently low temperature while the surface is still lighted. There is experimental evidence showing that there is movement toward a light at the top of a column of water when its lower strata are cold enough. But the laboratory results indicate that there is practically no upward movement in darkness or in diffuse light if the observations are made during the hours of daylight. In view

of these various results, it appears that the upward migration requires water of relatively low temperature and light at the surface.

But, according to the published results of the field work (Esterly, 1912, pp. 282–285), the accumulation at the surface is greatest from 8 P.M. to 12 P.M. It is reasonable to suppose that some of the upward journey is accomplished in very dim light or in darkness, and it is difficult to account for such behavior on an experimental basis. If we grant that the organisms in descending reach water of a temperature so low that they *begin* to ascend, I do not see how the continuation of the ascent is to be accounted for after the animals reach the warmer water at higher levels. The initial stages of the upward migration may take place in the colder water of the deeper strata, but some other factor is apparently necessary in order to account for the completion of the journey to the surface. This factor, as shown by the experiments, may be the physiological rhythm. It is possible that the ascent may be accomplished in the absence of *directive* stimuli.

If the descent takes place as day begins to dawn it is readily accounted for, on the basis of these experiments, by negative phototropism at the temperatures that prevail at the surface and by positive geotropism in light from above. Our field data show, however, that these copepods forsake the surface several hours before dawn (Esterly, 1912, p. 284), though our observations are admittedly inconclusive. If more complete information should establish this point the positive geotropism in darkness might explain the descent and there would be no need to attribute anything to a response to light. When the "physiological state" that prevails during the time that the animals show negative geotropism wears off or is changed the descent will begin.

It is certain that under natural conditions large numbers of these animals arrive at the surface in the dark and continue to be obtained there during several hours of darkness. Their ascent begins in water of lower temperature than that at the surface, and the water becomes continually warmer at higher levels until temperatures are encountered in which there should be negative phototropism, as shown by the laboratory results. The problem is to explain the ascending into warm water in darkness. I believe that the facts brought out in connection with the physiological or metabolic rhythm offer the best basis for the desired explanation. The cause of the rhythm is, in turn, a separate question.

An explanation of the diurnal migration of *Calanus* based on geo-

tropic and phototropic reactions is beset by too many difficulties to be readily acceptable in view of the results of field work. The matter of the rhythm affords a simpler way of accounting for the habit, but it ought to be supported by more evidence than that brought forward here.

In discussing the results of field work (Esterly, 1911, p. 148, 1912, p. 292) it was stated, as a matter of opinion, that light appears to be the chief factor in the diurnal movement. There was no evident correlation to be found between abundance of organisms and temperature and salinity (Esterly, 1912, pp. 292, 294). It must be said that on the basis of the laboratory results the effects of variation in intensity of light (apart from direction) are negligible so far as vertical movements are concerned. There is some change in behavior when the temperature is lowered and the source of light is at the top or at the bottom of the column of water. The reactions do not change significantly when the salinity is increased. It is evident, therefore, that the causal interpretations based on field results do not conform to the laboratory results. Likewise, it is difficult to arrive at an understanding of what *Calanus* does in nature if we use the results of these experiments as a basis for judgment.

It is not improbable that a reëxamination of the field data, which are now more extensive than when the papers referred to were written, will show correlations between abundance of animals and external conditions that come into line with the results of experiment. It is also not improbable that continued experimentation will show that certain of the responses are due to the artificial conditions of the laboratory, and will reveal others that conform to the facts shown by the field data.

Reactions of the copepod *Eucalanus elongatus*

This is an unusually large copepod, the length often being from six to eight millimeters. The body is of glass-like transparency, but in many animals there is a reddish or yellowish oil drop outside the digestive tube in the posterior part of the cephalothorax. The animals of this species are unique, so far as my experience goes, in that they do not have the incessant jerky movement so characteristic of copepods. A specimen of *Eucalanus* rests quietly for several minutes at a time, then suddenly darts away at such speed that it can hardly be followed with the eye. While resting the long anterior antennae are extended at right angles to the body, but when the animal swims they are folded

back against the body. There is another sort of movement, however, that is so slow it is barely perceptible. It is brought about by very gentle motion of the feet, some of the head appendages, and the abdomen. If the word "wiggle" may be used it serves to describe the action of the appendages. One is aware that there is a slow change of position, but it gives the impression of "creeping" or "drifting" as I have called it for myself. There are times, also, when none of the appendages are in motion, and then the body assumes almost any posture in the water; the head may be down or up, or the body tilted toward one side, so that a line passed through the extended antennae is neither horizontal nor vertical. It has seemed to me that the drop of oil in the body has something to do with the position taken; there is a tendency for the posterior end to gradually rise higher than the anterior end, and the oil drop is always nearer the posterior end. I believe that the "creeping" movement is due to the action of the appendages; I have not been able to determine that there is any change of position unless the appendages are moved. When an animal is in a vertical tube the "creeping" produces either ascent or descent.

If a specimen is in a shallow dish it can be gently moved about with a capillary rod so that the axis of the body takes any desired direction as regards the light. Under such circumstances one can easily see how the creeping will alter the position of the animal. The appearance is as if the body were drifting in a very gentle current of air over the surface. The animal moves in almost any direction, even sideways, or it swings around through part of a circle.

It does not seem to me that the so-called creeping movement is in the nature of a response. The direction of such movements is too irregular and aimless. They may lead to ascent or descent, or movement toward or away from the light, or in a line parallel to the window.

PHOTOTROPISM

Although the drifting is without definite direction, the other sort of locomotion is very definitely negative phototropism. The swooping dash is always away from the light. It takes place without any preliminary signs. If the head of the animal is directed toward the light one movement of extraordinary speed turns the body and carries the animal toward the side of the dish opposite the light. This behavior can be best observed in a shallow dish, but in a tube also the actual swimming is away from the light. Table 11 summarizes the results of the experiments; both the rapid and the slow movements are in-

cluded. All the tests were made in the light by the 50 by 40 cm. window of the darkroom.

TABLE 11

THE PHOTOTROPISM OF *Eucalanus*. SUMMARY OF INDIVIDUAL RECORDS IN ALL INTENSITIES. TEMPERATURE 16°–20°C; SALINITY 33 TO 34 $^0/_{00}$.

Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
					per cent of total showing					Per cent	
					movement		no movement				
		+	—	Total	+	—	+	—	Total (cms.)	+	—
73	9	45	100	184	11	69	20	0	1,432	3	97

It may be said that all the movements that show positive phototropism are due to the drifting, and if these records were omitted there would be only negative phototropism. But as the table stands the responses are strongly on the negative side.

GEOTROPISM

The movements of *Eucalanus* in a column of water are of the two general sorts. The animals "drift" up or down and also swoop in either direction.

Table 12 indicates the nature of the behavior in a vertical tube. The table summarizes records that were made at intervals of varying lengths, and the figures merely show the direction of movement without regard to the method by which it is brought about. Records that show no change of position are so few that they are omitted from the table.

TABLE 12

THE GEOTROPISM OF *Eucalanus* UNDER DIFFERENT CONDITIONS OF LIGHTING AND IN DARKNESS. SUMMARY OF INDIVIDUAL RECORDS. TEMPERATURE 16°–20°C; SALINITY 33 TO 34 $^0/_{00}$.

Number of experiments	Number of animals tested	Per cent of animals moving		Records of position			Distance		
					per cent of total showing movement			Per cent	
		+	—	Total	+	—	Total (cms.)	+	—
				IN DIFFUSE LIGHT					
35	5	100	100	223	58	42	1,637	67	33
				IN DARKNESS					
7	2	100	100	24	71	29	164	79	21
				IN VERTICAL LIGHT FROM ABOVE					
6	4	75	75	24	75	25	301	89	11
				IN VERTICAL LIGHT FROM BELOW					
8	5	100	100	27	22	78	203	8	92

The table shows, in brief, that *Eucalanus* is positively geotropic except when exposed to light from below. It is then strongly negative, and we may suppose that the negative phototropism is stronger than the tendency to move downward.

The responses were not investigated in water of unusually low temperature or high salinity, so that it is not known whether the phototropism and geotropism change as these factors are altered.

The experiments have shown that *Eucalanus* is strongly negative to light of low and of high intensity, and positive to gravity in diffuse light, in darkness, and in light from above. It is negatively geotropic in light from beneath. Since experiments are lacking to show whether these reactions change with decreased temperature or when the salinity is increased, it seems hardly worth while to discuss the bearing of the experimental results on diurnal migration. It may not be out of place to state that the reason for the few experiments with *Eucalanus* is that the animals were obtained in such small numbers. Practically all the individuals brought in were used.

The results of an examination of the field records for *Eucalanus* are available in two papers (Esterly, 1911*a*, 1912, pp. 295–300). The data show that there are larger numbers of animals at the surface at night, but it does not appear that there is a well marked diurnal migration although there is an extensive movement below the surface.

Reactions of the copepod *Labidocera trispinosum*

These animals have been extraordinarily abundant at times about La Jolla, but during the academic year 1916–17 they were scarce. The animals do not endure confinement in the laboratory very well, and they do not usually remain in suitable condition even over night. But if they were active on the second day after collection I did not hesitate to use them. I have not found any reason to suspect that the responses change after the animals are brought into the laboratory

Labidocera differs from the other copepods used in having well developed eyes with prominent lenses. There are two on the dorsal and one on the ventral surface of the head.

The animals are rather slow swimmers as a rule, but if disturbed they dart about with great rapidity. The movement is steady and lacks the jerkiness of *Calanus* or *Acartia*. When swimming in a shallow dish the course is wavering and uncertain but the animals keep moving steadily. In the narrower confines of a tube the course is prac-

tically straight. The posterior antennae are in constant motion whether the animal is ascending or descending in a vertical tube; in the latter case the appearance is something like that of a bird hovering. I have seen no instances in which an animal sank immobile after the fashion of *Calanus*. It is not uncommon for individuals to circle in a vertical plane, and sometimes this behavior is kept up for a good many minutes.

PHOTOTROPISM

Labidocera is negative to light. I have not tested them in a wide range of intensities but the reactions are predominantly negative in the dim light of a 15-watt lamp as well in that of the 50 by 40 cm. window. Table 13 is a summary of the behavior of several animals in a rectangular aquarium 20 by 8 cm. The vessel was marked off into five sections, as usual, and turned end for end several times in the course of an experiment.

TABLE 13

THE PHOTOTROPISM OF *Labidocera*. SUMMARY OF RECORDS OF SEVERAL SETS OF ANIMALS IN LIGHT OF NORTH WINDOWS; TEMPERATURES 15°–20°C, SALINITY 33 TO 34 ‰.

Whole number of animals observed	Percentage distribution in the sections					Number of observations			Center of distribution
	negative V	IV	III	II	positive I	Total	per cent showing more animals in: positive %	negative %	
304	85	5	4	1	5	24	0	100	4.6

Table 14 is of the usual form that deals with the responses of different individuals. The results of using different intensities of light are put together in the table since most responses are negative.

TABLE 14

THE PHOTOTROPISM OF *Labidocera*. SUMMARY OF RECORDS OF INDIVIDUALS IN LIGHT OF LOW AND HIGH INTENSITY. TEMPERATURES 15°–20°C; SALINITY 33 TO 34 ‰.

Number of experiments	Number of animals tested	Number of animals moving		Records of position					Distance		
					per cent of total showing					Per cent	
					movement		no movement				
		+	—	Total	+	—	+	—	Total (cms.)	+	—
110	23	17	100	284	10	70	4	16	3,821	5	95

The results that appear in tables 13 and 14 are so evident that comment is unnecessary.

GEOTROPISM

In darkness and diffuse light. It is difficult to know what to say about the geotropism of *Labidocera*. There is a good deal of difference in the behavior of different sets of animals. I used two sets of individuals. Lot A was obtained at 8 A.M. at the surface and had been in the laboratory six hours before the experiment began. Lot B was obtained in a vertical haul from about 60 meters at 9 A.M. and had been in the laboratory about two hours. Except for these differences the treatment and surroundings of the two sets were similar. Table 15 summarizes the observations on the distribution of the two sets in darkness and in diffuse light.

TABLE 15

The Geotropism of Two Sets of *Labidocera* (A and B) in Diffuse Light and in Darkness. Temperatures 15°–18°C, Salinity 33 to 34 ‰.

	Whole number of animals observed	Percentage distribution in the sections					Number of observations			Center of distribution
		top V	IV	III	II	bottom I	Total	per cent showing more animals in upper ⅖	per cent showing more animals in lower ⅖	
					In Darkness					
A	47	19	8	11	11	51	7	14	86	2.3
B	115	67	3	5	7	18	29	69	21	3.9
					In Diffuse Light					
A	56	0	0	2	5	93	8	0	100	1.1
B	71	34	14	14	7	31	17	47	35	3.1

The table shows that in darkness the animals of lot A were strongly positive in geotropism while those of lot B were even more strongly negative. In diffuse light lot A was very strongly positive and lot B predominantly but not markedly negative. Yet it is shown that with each set there is an upward movement in the dark. The totals of the percentages in sections IV and V are larger for both A and B in the first two lines of the table than in the last two lines, and those in sections I and II are smaller in the first two than last two lines of the table. The centers of distribution, likewise, show that there is ascent in darkness. Yet the two sets of animals are significantly different in behavior if the distribution in darkness or in diffuse light is considered alone It is upon comparison of the distribution under one condition with that under the other that the movement is indicated.

It does not seem that retention in the laboratory will account for the difference in the two sets of animals. Lot A was in the laboratory

for eight hours altogether and lot B for about eleven hours. But the latter animals were in darkness from the sixth to the eighth hour and were consistently and strongly negative and during that time twelve observations of the distribution was made. If something connected with the laboratory conditions affects the animals, it plainly does not affect all in the same way. In spite of the differences it appears, nevertheless, that there is a tendency for *Labidocera* to ascend in darkness, and to descend in the light.

Table 16 (p. 49) deals with the behavior as shown by the results with individual animals, the table being a summary. The possible effects of longer and shorter periods of confinement in the laboratory are considered by separating the recorded results into two groups for both darkness and diffuse light.

It must be said that the results appearing in table 16 are confusing. Negative geotropism prevailed slightly in diffuse light among animals that had been a shorter time in the laboratory (C), at least so far as the actual swimming is concerned. The reverse is indicated for animals that had been longer in the laboratory (D); all the percentages are in favor of positive geotropism. The results of tests in darkness, so far as they go, show that there is prevailing positive geotropism in animals that were in the laboratory from 1–3 hours. This is also the case in the second line of the table except as regards the distance covered, where the difference is strongly in the negative column. It is well to note that the distance percentages show that there is an upward movement in the dark of animals kept for the longer time in the laboratory (compare lines B and D), but the records of position do not show that. If lines A and C are compared it is seen that the distance percentage shows upward movement in the light, and this is also indicated by the differences in the percentage of records that show change of position.

In view of the discordant results in table 16, especially when they are compared with table 15, it is difficult to know what to conclude as to the geotropism of *Labidocera* in the absence of directive light.

In directive light. The tendency of *Labidocera* to move away from a source of light is shown, I believe, by its behavior in a vertical tube when a lamp is at the top or bottom. In the former case the responses are negative to light and positive to gravity; in the latter they are negative to both. The facts are shown in table 17 (p. 49). Length of time in the laboratory does not make any difference in the behavior apparently, so all records are entered in the table. The source of light

was the 15-watt lamp. It was placed about ten centimeters from the top or bottom of the container, which was in most cases a tube 500 by 30 mm.

So far as the observations that are summarized in table 17 are concerned it is evident that *Labidocera* ascends or descends depending on the location of the light.

SUMMARY

The experiments show: (1) That *Labidocera* is negatively phototropic at ordinary temperatures. The responses are negative to light of low as well as of high intensity. (2) The results concerning geotropism are confusing. Table 15 shows that there is a tendency to ascend in darkness and to descend in diffuse light on the part of specimens that had been in the laboratory for ten hours at the most. In table 16 it appears that there is a tendency toward negative geotropism in diffuse light when the specimens had been in the laboratory from one to six and a half hours; but those not tested for twelve to twenty-seven hours after removal from the sea show positive geotropism. Two individuals that were tested in darkness within one to three hours after they were taken from the ocean showed positive geotropism; others, not used until twelve to twenty-six hours after capture, gave uncertain results. (3) In directive light from above the geotropism is strongly positive; in directive light from below it is strongly negative (table 17).

POSSIBLE BEARING OF THE EXPERIMENTS ON DIURNAL MIGRATION

Since there is nothing to show whether the behavior changes when the temperature is lowered or the salinity increased, a full discussion of the relation between the results in the laboratory and the natural habit is not possible.

So far as the experiments are concerned, it is not to be expected that *Labidocera* will occur at the surface during the day since it is negatively phototropic and positively geotropic when the light is from above; also the field data show that this copepod is very much more abundant at the surface from 6–8 P.M., and that it is practically absent at other times (Esterly, 1912, pp. 307–309). The upward movement of some sets of experimental animals when in the dark

TABLE 16

THE GEOTROPISM OF *Labidocera*. SUMMARY OF INDIVIDUAL RECORDS IN DIFFUSE LIGHT AND IN DARKNESS. TEMPERATURES 16°–20°C; SALINITY 33 TO 34 ‰.

	Hours in laboratory	Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
							per cent of total showing					Per cent	
							movement		no movement		Total (cms.)		
				+	—	Total	+	—	+	—		+	—
						IN DARKNESS							
A	1–3	7	2	100	100	68	32	27	22	19	457	62	38
B	12–26	5	4	50	25	37	16	11	62	11	68	37	63
						IN DIFFUSE LIGHT							
C	1–6½	27	9	56	89	107	24	33	29	14	610	43	57
D	12–27	19	7	86	86	142	53	18	24	5	695	60	30

NOTE.—The individuals in A, C, and D were all different; the four in B were also used in C but not in A or D.

TABLE 17

THE GEOTROPISM OF *Labidocera* IN DIRECTIVE LIGHT. SUMMARY OF INDIVIDUAL RECORDS. TEMPERATURES 16°–20°C; SALINITY 33 TO 34 ‰.

Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
					Per cent of total showing					Per cent	
					movement		no movement		Total (cms.)		
		+	—	Total	+	—	+	—		+	—
				VERTICAL LIGHT FROM ABOVE							
16	5	100	0	34	80	0	20	0	745	100	0
				VERTICAL LIGHT FROM BELOW							
17	7	57	100	74	20	53	4	23	805	7	91

(table 15) is in line with the distribution observed in the sea, and the negative reactions to light account for the small numbers at the surface during the day. But the inconstant results obtained in experiments on the geotropism make difficult their application to the behavior of the species under natural conditions.

Reactions of the copepod *Metridia lucens*

The occurrence of this copepod as material for experiment was erratic, but the animals were obtained in fairly large numbers and at opportune times so that it was possible to work with them to advantage. The locomotion of these organisms is slow unless they are suddenly disturbed; there is nothing of the jerky character in the swimming; it is what may appropriately be called "sailing." This sort of movement is continual, but if the vessel is jarred the animals dart about with great rapidity. The sailing of *Metridia* is different from the "fluttering" or "hovering" of *Labidocera,* but the difference is hard to express in words. When specimens are in diffuse light in a vertical tube it is especially common when they are descending to see them sail in small circles that together make up a close spiral carrying them lower and lower. They also travel in vertical circles, something like "looping-the-loop" in an aeroplane, so that they gradually descend. Very rarely a specimen will drop down like *Calanus.* but practically always the animals are sailing about in circles. If a light is placed at the top of the tube it is not uncommon for the descent to be accomplished by swimming down head foremost.

Metridia lives very well under laboratory conditions, and I have not observed any difference in the behavior soon after they have been taken from the sea as compared with that several hours later.

Phototropism

The reactions have been observed in the light of the window 50 by 40 cm., in the 15-watt, at distances of ten, fifty, and one hundred centimeters from the end of the tube or side of a dish next the lamp, and in the light of the 100-watt lamp about 200 times the intensity of the 15-watt. *Metridia* is negative to each of these intensities at room temperatures and in water of usual salinity. Positive responses predominate, however, if the water is cooled to 10°C. Table 18 shows a summary of the results when several animals are under observation at a time.

TABLE 18

THE PHOTOTROPISM OF *Metridia* AT ROOM TEMPERATURE AND AT 10°C OR LESS

Whole number of animals observed	Percentage distribution in the sections					Number of observations			Center of distribution
	negative V	IV	III	II	positive I	Total	per cent showing more animals in positive %	per cent showing more animals in negative %	
TEMPERATURES 15°–20°C									
391	47	8	9	10	26	56	25	70	3.9
TEMPERATURE 10°C OR LESS									
78	1	0	6	3	90	13	100	0	1.2

So far as my observations go, the animals will remain positive indefinitely providing the water is kept cooled. There is more or less swimming back and forth under any circumstances; but most of the animals are on the side toward the light in cold water, and on the side away from the light in the warmer water. The same animals are positive, in cold water, to the light of a 15-watt lamp and also to that of a 100-watt that is 200 times as intense. The movements away from the light when its intensity is low (the 15-watt at 50 or 100 cm.) do not begin as promptly as when the animals are exposed to the light from the window, and progress is slower at the lesser intensities.

When individual animals are used the results (table 19, p. 53) are similar to those set forth for the higher temperatures in table 18.

The table shows that the negative greatly outnumber the positive responses, while the distance covered is practically all in the negative direction.

GEOTROPISM

Table 20 (p. 53) gives the summary of results obtained when several animals were under observation at once. It shows the difference in behavior in water of low and high temperature. In all the experiments with cold water the entire tube or cylinder was in ice water, at temperatures ranging from 7°C to 9°C.

In diffuse light there is strong tendency for the animals to descend or to stay at lower levels when the temperature is that of the room. It is suggested by the results that negative geotropism is somewhat increased in the cold water.

In darkness the geotropism changes as the temperature changes. It is strongly positive at the higher temperatures, and strongly negative in cold water. If the animals are at the bottom in cold water when the light is extinguished they ascend and remain at or near the top;

their negative geotropism involves both locomotion and maintenance of position at high levels. If they are in section V when subjected to darkness they do not descend, providing the temperature is low enough.

When exposed to light from above in water of room temperature the animals descend and remain at the bottom. But in the cold water they ascend toward the light and remain at the top or near it. In light from below, however, there is a marked movement upward at room temperatures; at low temperatures, on the other hand, the animals will descend toward the light and remain in the bottom sections.

Inspection of the figures in table 20 showing the centers of distribution reveals the difference in distribution of the animals as the temperature is higher or lower

The results obtained with individual animals are confirmative of those with sets of animals, although no tests at low temperature were made in the former case. Table 21 (p. 55) deals with such records and it shows that the dominant response is positive geotropism in all conditions except when the light is below.

SUMMARY

The experiments show: (1) That *Metridia lucens* is negative to light at ordinary temperatures, but positive if the water is cooled to 9°C. (2) The animals are positively geotropic at ordinary temperatures in darkness and under any condition of illumination except light from below, and these responses are reversed in cold water.

POSSIBLE BEARING OF THE EXPERIMENTS ON DIURNAL MIGRATION

It is safe to say that so far as these experiments go they offer a ready explanation of some phases of the vertical migration. *Metridia* is negative to light and is positively geotropic (except when lighted from below) at temperatures ranging from 16°C to 19°C. Both the geotropism and phototropism are reversed at 9°C.

Now if the animals in the sea descend to sufficient depths they will encounter temperatures in which the direction of movement is reversed and it may be expected that they will begin to ascend. The field data show that these copepods are found in largest numbers dur-

TABLE 19

THE PHOTOTROPISM OF *Metridia*. SUMMARY OF INDIVIDUAL RECORDS. TEMPERATURES 16°20°C; SALINITY 33 TO 34 ‰.

Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
					Per cent of total showing					Per cent	
					movement		no movement		Total (cms.)		
		+	—	Total	+	—	+	—		+	—
33	9	22	100	83	2	94	4	0	798	1	99

TABLE 20

THE GEOTROPISM OF *Metridia* UNDER DIFFERENT CONDITIONS OF LIGHTING AND IN DARKNESS, AND AT LOWER AND HIGHER TEMPERATURES

Temperature	Whole number of animals observed	Percentage distribution in the sections					Number of observations			Center of distribution
		top V	IV	III	II	bottom I	Total	per cent showing more animals in upper ⅖	per cent showing more animals in lower ⅖	
IN DIFFUSE LIGHT										
16°–19°	354	15	6	7	9	63	59	20	76	2
7°–9°	32	44	0	0	6	50	4	0	50	2.8
IN DARKNESS										
16°–19°	570	8	2	7	10	73	92	2	98	1.6
7°–9°	102	63	12	6	9	10	13	85	8	4.1
IN VERTICAL LIGHT FROM ABOVE										
16°–19°	186	2	11	11	10	66	28	14	82	1.7
7°–9°	112	77	11	4	3	5	15	93	0	4.5
IN VERTICAL LIGHT FROM BELOW										
16°–19°	370	42	8	6	5	39	52	54	42	3.1
7°–9°	141	13	8	6	8	65	18	8	92	1.7

ing the day at about 270 meters (Esterly, 1912, pp. 304–305), and according to McEwen (1916, pl. 34) the mean annual temperature at that depth is between 8° C and 9° C; at such temperatures in the laboratory the phototropism changes from negative to positive and the geotropism from positive to negative. If it is assumed that when the animals in the ocean reach water of 10° C they begin to ascend, the ascent into warmer water remains to be accounted for; this point is not covered by the experiments. We know, however, from the field records that *Metridia* is found in great numbers at the surface when the temperature is 19° C (Esterly, 1912, p. 306). If the ascent begins in a region of lower temperature, why does it continue into water of temperatures in which experimental animals are positively geotropic? It is possible that the answer to this question will be found in the occurrence of a physiological rhythm, but I have no evidence that the rhythm is present in *Metridia.*

Reactions of the chaetognath *Sagitta bipunctata*

A study of the reactions of this animal seemed especially desirable because of the striking results obtained from the field data, as shown by the study made by Michael (1911). He has shown that there is marked correlation between occurrence of this species and variations in certain external conditions, and the question at once arose whether similar behavior would be shown in the laboratory.

So far as I am aware, a chaetognath has never before been used in experiments on behavior. *Sagitta* is usually to be obtained at La Jolla in sufficient abundance if the collecting is done at depths of 75–100 meters. The animals come far enough toward shore to be taken from the pier, but occurrence there is exceptional.

A great deal of difficulty was experienced in obtaining specimens in the proper condition for experiment. On many occasions they show signs of morbidity even before they reach the laboratory. The body becomes slightly opaque or milky and bits of sand and débris adhere to the exterior. Moreover, the animals rest quietly on the bottom of the dish if they are in bad condition, instead of swimming around constantly. I soon learned that an animal that has sunk to the bottom will not react.

The reasons for the appearance of such unfavorable states are not clear. Our success was much better if a two-quart jar was tied into

TABLE 21

THE GEOTROPISM OF *Metridia*. SUMMARY OF INDIVIDUAL RECORDS. TEMPERATURES 16°–20°C.; SALINITY 33 TO 34 ‰.

Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
					Per cent of total showing					Per cent	
					movement		no movement		Total (cms.)		
		+	−	Total	+	−	+	−		+	−
				IN DIFFUSE LIGHT							
11	6	100	50	71	77	21	0	2	353	82	18
				IN DARKNESS							
4	2	50	50	18	50	22	28	0	117	85	15
				IN VERTICAL LIGHT FROM ABOVE							
7	5	100	0	17	100	0	0	0	254	100	0
				IN VERTICAL LIGHT FROM BELOW							
10	5	80	80	57	28	53	10	9	275	31	69

the net so that the animals passed into a larger amount of water than when a bottle was used. But perfectly satisfactory material has been obtained in the latter case, and very poor in the former. Water from the laboratory supply, as contrasted with that carried in from the pier, is not always to be blamed. One animal lived for three days in sea water drawn from the pipes, without changing the water, and the specimen was apparently in as good condition on the third day as on the first. Its death was due to exposure to direct sunlight. If the animals are in good condition handling them does not have an unfavorable effect. It is necessary to pick them up with a pipette, and this must be done carefully of course, but it does not interfere with their activities. Pouring from one dish to another is not injurious.

On the whole, I do not know of anything that will insure one's having good material. It must be taken as it comes. Specimens can practically always be obtained but their condition is problematical. With identical treatment they may at one time be perfectly satisfactory and at another be the opposite.

Sagitta is not a particularly rapid swimmer, even when disturbed, as by the approach of the pipette. The animals are expert "dodgers," and this combined with the transparency of the body makes it difficult to catch them. Swimming is accomplished by making strokes with or by "flirting" the tail. At each stroke the animal moves forward a short distance, and this action is kept up continually. The animals can even swim backward by what is to all appearances the same method of propulsion as that used for locomotion in the opposite direction.

Another difficulty met with in using *Sagitta* is that of seeing the animals, particularly in a large dish of water. It is not hard to keep track of an individual nor to count a number of animals in a tube when one can look through the water toward the light. I found it impossible to do anything, however, by looking down into a dish of water from above.

I believe that there need be no hesitation in using animals that have been in the laboratory, so long as they are swimming about; that is the best test of condition I have found. I did not reject specimens even on the second day, and I think that their reactions then are as characteristic of the species as those of any animals in the laboratory.

TABLE 22

THE PHOTOTROPISM OF *Sagitta*. SUMMARY OF INDIVIDUAL RECORDS. TEMPERATURES 16°–20°C; SALINITY 33 TO 34 ‰.

Number of experiments	Number of animals tested	Per cent of animals moving		Records of position					Distance		
					Per cent of total showing					Per cent	
					movement		no movement				
		+	—	Total	+	—	+	—	Total (cms.)	+	—
38	14	100	29	204	70	19	6	5	428	97	3

TABLE 23

THE GEOTROPISM OF *Sagitta* UNDER DIFFERENT CONDITIONS OF LIGHTING AND IN DARKNESS. SUMMARY OF INDIVIDUAL RECORDS. TEMPERATURES 16°–20°C; SALINITY 33 TO 34 ‰.

Number of experiments	Number of animals tested	Number of animals moving		Records of position					Distance		
					Per cent of total showing					Per cent	
					movement		no movement				
		+	—	Total	+	—	+	—	Total (cms.)	+	—
				IN DIFFUSE LIGHT							
30	8	50	87	142	12	50	8	30	922	11	89
				IN DARKNESS							
16	6	16	66	60	2	23	0	75	671	1	99
				IN VERTICAL LIGHT FROM ABOVE							
22	9	66	78	105	28	41	1	30	902	30	70
				IN VERTICAL LIGHT FROM BELOW							
26	8	75	63	120	30	38	11	21	838	37	63

PHOTOTROPISM

The evidence that I can present regarding the reactions of *Sagitta* to light has all been obtained by observing individual specimens. So far as my records go the animals are strongly positive to light if they are in a horizontal tube that is parallel to the rays. In a stock dish before the window it seems to me that the specimens are swimming around indiscriminately, but the difficulty of observation under such circumstances is great. Table 22 (p 57) is a summary of the observations. All were made upon animals in the 50-centimeter tube. As soon as a specimen reached the end of the tube it was turned to the vertical position and the geotropism noted. The observations were made in intensities ranging from bright daylight, through the 50 by 40 centimeter window, to the 15-watt lamp at 10, 20, and 50 centimeters; the 100-watt lamp was not used.

The table clearly shows that the animals react positively to light. There is no reason to doubt that after moving as far as possible toward the light they would remain there. Some observations have shown that an animal may actually turn about and swim away from the light for a short distance, and then turn and swim toward the light. The behavior toward light was not tested in water of low temperature or high salinity.

GEOTROPISM

When the individual records are summarized it appears that there is a well defined negative geotropism at ordinary temperature and salinity. There is evidence that the geotropism changes in diffuse light of too great intensity, but in the dark room with the window unshaded or in the light of the 15-watt lamp, the animals ascend and remain at or near the top. The same is true of the behavior in darkness and in vertical light from below and from above. Table 23 (p. 57) gives the summary of results of observations on single specimens.

It seems to me that the evidence is conclusive that *Sagitta* is negatively geotropic in darkness as well as in light from any direction and of the intensities used in the experiments. When once at the top the animals keep bumping against the end of the tube, and if they stop swimming they drop down for a longer or shorter distance and then swim back to the top; this passive descent accounts for most of the records that show downward movement. When the tube is lighted

from below it is not unusual to see an animal swim down toward the light. When the tube is lighted from above I have seen animals swim from the bottom to the top, then drop from the top to the bottom, and after a few moments return to the top and stay here. In no case, however, has an animal descended by swimming except when the light was beneath.

When *Sagitta* is in a vertical tube that stands in a room with white walls and several high windows he negative geotropism changes to positive. The following case is a good illustration of this. A tube containing an animal that was positively phototropic to the light from the large window of the dark room, and negatively geotropic in darkness as well as in the diffuse light of the dark room, was carried out into the main laboratory. The light was much brighter there because of several large windows and white walls and reflection from the windows and walls of an adjacent building. In this light the specimen would swim down slowly and was also negatively phototropic. When the tube was shaded by the door of a closet, the animal would turn and ascend. If the tube was moved into the brighter light while the specimen was still swimming up, it turned and swam down, and if put into the subdued light while still descending the course was reversed. This was repeated several times with this particular animal, and I have no doubt that such behavior is characteristic of the species.

Confirmatory results have been obtained with several animals under observation at once. The specimens descend in the light of a room with white walls and three tall north windows, and they ascend in the dark. There are two different experiments to be reported on, and table 24 (p. 60) deals with the first of these. There were fourteen animals, obtained half an hour before the experiment began, in a cylinder 50 by 6 centimeters that stood 75 centimeters from the windows. A light proof box was set over the cylinder when it was desired to subject the animals to darkness; otherwise they were in the bright diffuse light of the room. The column was marked off into five divisions. Only those animals were counted in the lowest section that were actually off the bottom, so that all the records dealing with distribution relate to animals that were able to swim. In addition to giving a summary of the distribution, table 24 outlines very briefly the changes in external conditions.

TABLE 24

The Geotropism of *Sagitta* in Bright Diffuse Daylight and in Darkness, and Under Varying Conditions of Temperature.

Salinity 33 to 34 ‰.

	Whole number of animals observed	Percentage distribution in the sections: top V	IV	III	II	bottom I	Number of observations: Total	Per cent showing more animals in: upper ⅖	lower ⅖	Center of distribution
		11:15 a.m.–3:15 p.m., darkness, temperature 16°–17°C								
1.	147	28	15	1	9	47	12	17	58	2.7
		3:15–3:20 p.m., diffuse light, temperature 16°–17°C								
2.	18	5.5	5.5	0	0	89	2	0	100	1.4
		3:21–8:45 p.m., darkness, temperature 17°–18°C								
3.	80	50	18	10	6	16	7	100	0	3.8
		Left in dark overnight; following records obtained on second day of captivity								
		7:45–8:25 a.m., darkness, temperature 16°–17°C								
4.	33	61	15	9	0	15	3	100	0	4.0
		8:26–9:10 a.m., diffuse light, temperature 16°–17°C								
5.	38	2.5	8	2.5	18	69	5	0	80	1.6
		9:11–9:30 a.m., darkness, temperature 16°–17°C								
6.	20	55	20	0	5	20	2	100	0	3.8
		During time of lines 7–10, the lower one-fifth was at temperature of 7°–8°C								
		9:42–10:20 a.m., darkness								
7.	44	40	5	7	25	23	5	40	60	2.9
		10:21–10:40 a.m., diffuse light								
8.	35	6	0	14	69	11	4	0	100	2.2
		10:41–10:52 a.m., darkness								
9.	17	41	30	18	0	11	2	100	0	4.1
		10:53–11:07 a.m., diffuse light								
10.	17	11	18	53	18	0	2	5	5	3.2
		Ice jacket removed								
		11:08–11:20 a.m., diffuse light, temperature of lower one-fifth, 8⅔°–10⅔°C								
11.	18	6	17	11	33	33	2	0	100	3.6
		11:30 a.m., diffuse light, temperature of lower one-fifth is 12⅔°C								
12.	8	0	12	0	38	50	1	0	100	1.7
		11:30 a.m.–12:45 p.m., diffuse light, temperature of lower one-fifth goes up to 16°C								
13.	25	0	4	4	12	80	3	0	100	1.6
		12:45 p.m., lower one-fifth immersed in ice water								
		12:55–1:40 p.m., diffuse light, temperature of lower one-fifth 7°–9°C								
14.	23	0	22	4	39	35	3	0	100	1.9
		1:40–2:00 p.m., diffuse light; 2:00–2:15 p.m., darkness, ice jacket removed								
		2:15–2:30 p.m., darkness, temperature of lower one-fifth 10°–11°C								
15.	25	52	24	20	4	0	3	100	3	4.2
		2:30 p.m., lower three-fifths in ice, darkness								
		2:50 p.m., darkness since 2:30 p.m., temperature of lower three-fifths 8°–10°C								
16.	8	100	0	0	0	0	1	100	0	3.9
		2:50–3:25 p.m., diffuse light, temperature of lower three fifths 7°–9°C								
17.	32	22	44	0	0	34	4	75	0	3.2
		3:25–8:25 p.m., darkness, ice jacket removed								
		5:30–8:20 p.m., temperature of whole column 15°–16°C								
18.	26	70	15	4	4	7	3	100	0	4.3

The first six lines of the table show clearly that the experimental animals are positively geotropic in the light and negatively geotropic in the dark. It is true that during the first four hours of the experiment (line 1) most of the animals while in darkness were in the lower two-fifths of the cylinder; but by comparison they were less strongly positive than they were in the light (line 2). It is possible that we have to deal here with effects that are due to removal from the ocean; or it may be that there is some indication of a physiological rhythm. Neither of these possibilities has been investigated, but the general facts as to the behavior in light and in darkness are clear.

The change in distribution that occurs when the temperature is decreased appears in lines 7–10. The lower section of the cylinder was immersed in ice water. The figures show that while the animals ascended and descended as before, they did not go down into the cold water in the light. The largest numbers were found in the second section from the bottom (line 8) and in the middle section (line 10), and this can only be due, apparently, to the cessation of the descent that takes place when the animals enter cold water. Such behavior in diffuse light is in sharp contrast to that shown in lines 2 and 5; the temperature throughout the cylinder was about 17° C during the time those records were obtained.

From 11:08 A.M. to 12:45 P.M. the temperature of the lower section gradually increased after the ice was removed (lines 11–13). The numbers of animals in the bottom section constantly increased and the center of distribution was situated at successively lower levels. At 12:45 P.M. the container was again set into ice water so as to cover the bottom section, the lighting being unchanged. There is some suggestion in line 14 that the animals moved up from the lowest section as the temperature decreased but this point needs more evidence. The same thing is suggested again, however, if line 15 is compared with line 16. In both cases the animals were in darkness, but they very evidently moved upward when the lower three-fifths of the column of sea water was chilled. At any rate that was the only external change that took place. It is probably shown in line 17 that some animals descend in diffuse light even through thirty centimeters of cold water; but it is noticeable that two-thirds of them remained in the two upper sections. Evidently the descent is checked by the low temperature. It should be stated that there is a possibility that the animals recorded in section I in line 17 were there previously but were not observed to be off the bottom; that is, there may not have been any downward move-

ment through the cold water leading to the distribution recorded in line 17 as compared with that in line 16.

Line 18 is of interest as showing that *Sagitta* may remain negatively geotropic in darkness for five hours; at least it may reasonably be assumed that there was no marked downward movement from 3:25–8.20 P.M.

Table 24 shows finally that specimens of this chaetognath may exhibit the same kind of behavior late on the day after their removal from the ocean that they did within the first hour.

In giving the results of similar experiments on a second set of twenty animals it is not necessary to go into so much detail as in table 24. The observations are summarized in table 25; there were alternating periods of diffuse light and darkness and all the records obtained under each condition are put together in the several divisions of the table. The experiments were carried on in a room with white walls and lighted by four tall north windows. The container was a cylinder 50 by 6 centimeters and the animals were put into it within half an hour of the time they were taken.

There is always more marked negative geotropism in darkness than in the light, regardless of the temperature. This is shown by the percentages and also by the centers of distribution. But it is evident that most of the animals do not descend in the light into the colder water. In sections *b* and *c* of the table most of the animals are shown to be in that fifth of the cylinder which is immediately above the upper limit of the cold water, during the time that the specimens were exposed to the light. In the first line of *b* in the table a larger proportion of animals is recorded in the middle section of the cylinder than in all the others in *c* most of the animals were in the upper section during the time they were in the light. When the temperature of the lower sections of the cylinder was higher more animals descended into those levels in the light.

SUMMARY

It has been shown by the experiments: (1) *Sagitta* is strongly positive to light ranging from that of a 15-watt lamp at 50 centimeters to daylight about 3800 times as intense. No tests were made with intensities beyond these limits. (2) The geotropism is predominantly negative in darkness and in light that is not too bright. In a room with white walls and well lighted from without the geotropism

TABLE 25

THE GEOTROPISM OF *Sagitta* IN BRIGHT DIFFUSE DAYLIGHT AND IN DARKNESS UNDER VARIOUS CONDITIONS OF TEMPERATURE. SALINITY 33 TO 34 ‰.

Whole number of animals observed	Percentage distribution in the sections					Number of observations			Center of distribution	Remarks
	top V	IV	III	II	bottom I	Total	Per cent showing more animas in upper %	Per cent showing more animas in lower %		
				a. 10:35 a.m.–12:45 p.m., whole column 17°–18°C						
97	27	12	11	6	44	5	20	80	2.7	Diffuse light
54	41	30	11	4	14	4	100	0	3.8	Darkness
				b. 1:10–1:35 p.m., lower two-fifths at 7°–9°C, upper three-fifths at 17°–18° C						
41	17	2	59	5	17	4	25	25	2.7	Diffuse light
19	74	5	5	5	11	2	100	0	4.2	Darkness
				c. 1:55–255 p.m., lower four-fifths at 7°–9°C						
94	60	12	5	8	15	11	100	0	4.0	Diffuse light
19	85	5	5	5	0	2	100	0	4.7	Darkness
				d. 3:05–4:25 p.m., lower four-fifths rises to 14°C						
48	23	4	4	8	61	6	0	100	2.2	Diffuse light
45	38	18	9	13	22	6	83	16	3.3	Darkness

is strongly positive. (3) The animals do not descend into water of 10° C except in small numbers; if the lower part of a cylinder of sea water is chilled most of the animals remain in regions above the level of the cold water although they are in the same intensity of light in which they descend if the water is warmer. The upward movement in darkness is not restricted, however, by such low temperatures.

POSSIBLE BEARING OF THE EXPERIMENTS ON DIURNAL MIGRATION

If these experiments suggest to any extent what the animals do in nature and reveal why they do it it is to be expected that the chaetognaths will desert the surface of the sea as the light grows brighter with the advancing day. It also seems clear that the descent will be checked as the animals reach colder water, and in the more subdued light they may begin to ascend. It is to be noted, in this connection, that the geotropism does not change as the temperature is altered; on the contrary, the direction of vertical movement is reversed as the light varies. The most that can be said with regard to temperature is that the animals do not descend into cold water; the descent is checked but the animals do not turn and ascend unless the intensity of the light is reduced. I think it is evident that the experimental results offer a basis for explaining the diurnal migration in its general outlines. Light intensity is apparently the determining factor; and it may be that this will explain some of the irregularities in the occurrence of the species at the surface mentioned by Michael (1916, p. xiii), where it is stated that large numbers have been obtained at the surface at all times of day and night and even at noon. The suggestion from the experiments is that on the occasions when there are many animals at the surface at noon the light is of comparatively low intensity, as on a cloudy day.

The distribution of *Sagitta* as regards different conditions in the sea has been very thoroughly studied by Michael (1911). The summary of facts derived from the study of field data (p. 157) shows that this species of chaetognath is found in unusually large numbers at the surface twice during the twenty-four hours, within an hour after sunrise and also within an hour after sunset. Below 25 fathoms it is most abundant between 10 A.M. and 2 P.M. The species is most abundant between the surface and 20 fathoms. Michael states (1911, p. 128, for example) that the facts of marked decrease about sunrise

and of marked increase soon after sunset "strikingly confirm our former inference that *S. bipunctata* migrates toward the surface during subdued light and away during intense light and darkness." The experiments confirm this statement in all respects except that the animals in the laboratory are negatively geotropic in darkness.

The distribution of *S. bipunctata* with regard to temperature shows (Michael, 1911, p. 133) that it is found in larger numbers at the surface when the temperature is low (15°.9 C–17°.5 C). "It is further suggested that low surface temperatures *retard downward* and *aid upward* migrations, and that high surface temperatures *retard upward* and *aid downward* migrations." It has been shown by the experiments that downward migration is retarded by low temperature, and there is some evidence in table 24 that there is more of an upward movement in darkness as the temperature is decreased than when it remains at 16° C or 17° C. This is an instance where experiment has verified a suggestion gained from a study of the field records. But the upward movement of animals in subdued light in an experiment is not held back by temperatures as high as 18° C; it is possible, however, that at 20° C the ascent would be checked, as suggested by Michael.

Since the field records and the experiments both show that in light of too great intensity there is downward movement, the question arises, How far will the animals descend under natural conditions? Michael (1911, p. 117) concludes that this chaetognath is rarely found below 75 fathoms and he states (p. 128) that it is most abundant between 40 and 75 fathoms from 10 A.M. to noon. For this discussion we may assume that 75 fathoms is the lower limit of the descent. The mean annual temperature at that depth (McEwen, 1916, pl. 34) is about 10° C, and this checks well with the observation in the laboratory that the animals do not descend into water that is cooled to 9° or 10° C. It cannot be stated at this time whether the downward movement stops at 75 fathoms because of the low temperature or because of the decrease in light intensity. The latter factor may be the determining one. Michael (1911, p. 158) has concluded that the region where the largest number of optimum conditions are found is from 15–20 fathoms. At that level the mean annual temperature is between 13° C and 14° C, and it is doubtful if the descent would be retarded at that temperature.

I believe that the results of these experiments and of the field work check each other in essential matters, in showing the conditions under

which *Sagitta bipunctata* ascends and descends, and why the downward migration does not extend deeper than 75 fathoms.

Since there are no experiments dealing with reactions in water of high or low salinity there does not seem to be any value in discussing the distribution of *Sagitta* in the sea as regards variations in salinity.

GENERAL DISCUSSION

The Effects of Laboratory Conditions in General on Experimental Animals

In the preceding accounts of responses it was pointed out that there is a noticeable change in the *kind* of reaction to light in the copepod *Calanus finmarchicus* and to both light and gravity in *Acartia tonsa* after the specimens have been kept in the laboratory for a time. To my mind this change is due to something connected with the artificial conditions under which the animals must be maintained, combined with the effect of removal from the ocean. Similar changes have been recorded by other observers in the case of other kinds of organisms. Harper (1905, p. 445) states that specimens of *Corethra* will collect on the lighted side of a dish when they are first brought in, and that this positive reaction gradually changes to negative. According to Jennings (1904, p. 83) certain rotifers show a like change; and there is a similar statement with regard to the copepod *Temora longicornis* by Loeb (1893, p. 94). Phipps (1915, p. 215) found that there is something associated with captivity that affects the phototropism of amphipods.

Such observations as have just been mentioned ought to make one question how far reactions that take place under laboratory conditions are likely to indicate the reasons for natural habit. If one is interested in what the specimens at hand are capable of doing under experiment it is desirable to allow them to "become accustomed" to laboratory surroundings. But if experimental results are sought for the information they may give concerning what the animals actually do *in nature,* it is necessary that the change in behavior be considered. What shall be said, for instance, about such a case as that of *Calanus?* The animals are positive to light at first, then they become permanently negative at room temperatures. The meaning of such a reversal ought to be considered. It may indicate that the state of the animals has returned to the condition that prevailed at the time of capture, and

which was upset by removal from deep water to the surface. If this is true there is no reason why the reactions observed in the laboratory should not be looked upon as affording a basis for ascertaining the factors that determine the migration. On the other hand, it may well be that the physiological state has *not* changed so long as the animals react positively to light, and that the change from positive to negative phototropism is the outward evidence of a condition that is the opposite of that prevailing at the time of capture. If this is really the case it seems plain to me that interpretations based on reactions will be erroneous.

Although it is not known just what the reversal in phototropism means, the fact that the change takes place should not be neglected. The purpose of observing the animals under laboratory conditions was to discover if possible why they are found during the day at 100 meters, for example, instead of at the surface. How can we expect to learn from the responses of a few representatives why the species as a whole is in deep water during the day unless the responses are evoked from animals that are in the same physiological state at the time of experiment as when they were swept into the net in deep water?

It must be admitted that the prevailing negative phototropism of *Calanus* appears to explain the absence of the animals from the surface during the day: they descend because they move away from the light. But is this true for animals in the sea? Specimens that are put under observation as soon as possible after they are brought to the surface are *positive* to light. Does that kind of response reveal the physiological condition of the specimens as it was at the level where they were obtained? If it does, we are prohibited from saying that the animals leave the surface because they are negative to light. As I look at this matter, we should consider whether or not the animals when brought to the surface have the same form of response that would be observed if it were possible to perform the experiments at a depth of 100 meters, for example. My own opinion is that the removal of the animals from deep water to the surface temporarily upsets the physiological state, and the brief period of positive phototropism is the sign of the disturbance. I believe that the animals when at 100 meters are really negatively phototropic. A good deal could be learned about the matter by comparing the behavior of animals from the surface with that of specimens from deep water. Experimental material of *Calanus* has not yet been obtained from the surface. But it may

reasonably be expected that the reactions of surface animals will be different from those of specimens from deep collections.

The behavior *Acartia tonsa* shows clearly how different the behavior of surface and deep water animals can be. This matter has been dealt with before (Esterly, 1917*a*, and also in this paper), but it is worth emphasizing again. This copepod is positive to light and negative to gravity in the light and positively geotropic in the dark, providing the specimens come from the surface. But animals that are obtained in deeper water (10–20 fathoms) are negatively phototropic and positively geotropic soon after capture both in diffuse light and in darkness. In this case, furthermore, there is a marked change in the behavior of specimens from deep water after they have been in the laboratory, for they come to react in all respects as do the animals from the surface.

I have not had the opportunity to compare the reactions of specimens from the surface and low levels of other forms than *Acartia*. It seems to me, however, that the results with that species are suggestive of possibilities in other forms. They show that the physiological state really is different, depending on the habitat from which the experimental specimens are obtained. What is true of one species is not necessarily true of another, but it is difficult to avoid the conclusion that the effect of laboratory conditions must be considered. At any rate an observer should look for the evidences of change in physiological state that may be connected merely with confinement in the laboratory before he uses experimental results to explain habits in nature.

Specificity in Behavior

Diurnal migration is a complex natural phenomenon in which many different kinds of organisms take part. The cause of the migration in each species is a particular problem, and there is need to realize that the facts of behavior of one form may not apply to others. A general explanation of the movement is desirable, of course, and the matter may be approached from the experimental side with a working hypothesis in mind. But a 'blanket explanation' will lead to controversy unless it is based upon experimental results obtained from a wide range of organisms. It is necessary to work first on *specific* problems since the phenomena recorded and the animals studied are so varied. An explanation based on the results of experiments with one sort of copepod can not be assumed to be applicable to another or

to a chaetognath. It may not be out of place to state that the experiments that have been reported here were conducted without preconceived ideas as to the reasons for the migration. It was my belief, and still is, that it is possible to learn from laboratory experiments why a species shows rhythmic vertical movements in nature. But it has become more and more apparent that specific differences in reactions must be taken into account. I am not yet ready to state that I believe a general explanation of diurnal migration is possible. It seems evident to me, as Parker (1902, p. 122) has already said, that the simultaneous depth-migration of different organisms may really be the results of quite different causes. It is probably understood that reference is made here to the sum total of the responses rather than to the behavior with respect to any one external factor.

In order to show the differences between different animals the following brief summary of results is given. It is based entirely upon these particular experiments and no reference is made to the behavior in water of high salinity since that was tested only with *Calanus*.

PHOTOTROPISM

Acartia: very strongly positive at room temperature with surface animals; deep water specimens are strongly negative; surface animals become negative in cold water, *A. clausi* to a greater degree than *A. tonsa*. *Calanus*: strongly negative to all intensities used at ordinary temperatures, becomes strongly positive at 10° C and less. *Eucalanus*: very strongly negative; effects of cooling not known. *Labidocera*: markedly negative; effects of cooling not known. *Metridia*: strongly negative at ordinary temperatures; becomes positive when water is cooled to 10° C. *Sagitta:* very strongly positive, behavior in cold water not known.

GEOTROPISM

Acartia: both species, if the animals are obtained from the surface, are markedly negative in the diffuse light of a room, but positive in darkness, and there is an increase in negative geotropism in darkness if the water is cooled to points below 15° C; specimens from deep water are very strongly positive in diffuse light and in darkness; there is a well marked physiological rhythm in geotropism if the animals are kept in darkness. *Calanus:* at ordinary temperatures the animals are very strongly positive in darkness and under all conditions of lighting, except that when lighted from below the positive geotropism is de-

creased; there is some reversal in cold water (10° C), especially when the light is above; there is some evidence of a rhythm in the reactions of specimens kept in very dim light, but only in case the bottom water, at least, is chilled. *Eucalanus:* strongly positive at ordinary temperatures except when lighted from below, then strongly negative; behavior at low temperature not known; possibility of rhythm not investigated. *Labidocera:* it is safe to say that there is a tendency to negative form of response in darkness and to positive in diffuse light; strongly negative in light from below, strongly positive in light from above; behavior at low temperatures unknown, and existence of rhythm not investigated. *Metridia:* at ordinary temperatures it is strongly positive in darkness and in all conditions of lighting except from below, then strongly negative; the behavior shows reversal at low temperatures; existence of rhythm not investigated. *Sagitta:* if light is not too bright there is marked negative geotropism under all conditions and in darkness; in bright diffuse daylight the response is markedly positive; the animals do not descend in cold water, but the ascent occurs in darkness out of cold water as well as out of warmer.

There are of course similarities in the behavior of different forms, and this is to be expected. For instance, *Calanus, Eucalanus, Labidocera* and *Metridia* are negative to light at room temperatures; *Acartia* and *Sagitta* are positive; *Calanus* and *Metridia* become positive on cooling, *Acartia* becomes negative. It is recognized that the experimental work is incomplete, particularly in that the behavior of *Eucalanus* and *Labidocera* in cold water is not known. But even so, if the behavior as a whole, or the sum of the responses, is considered in the cases of *Acartia, Calanus, Metridia,* and *Sagitta* it is very clear that each species has its own mode of action. It is possible, of course, that as more is known about the responses of the different forms the differences will tend to disappear; and it is likewise possible that when more is known still other differences will appear. But as the results stand it is plain that a general explanation based on laboratory responses can not be given that will cover the diurnal migration for the different species. Such an explanation is desirable, but it is necessary to recognize that when many different kinds of organisms perform depth migrations, it is likely that the end results are due to quite different causes.

The matter of specificity in behavior has been referred to in publications from the Scripps Institution that deal with the result of field investigations. Michael (1913, pp. 32, 36) has shown that manner of distribution is as much a specific character as structure; and he refers

(1916, pp. viii, ix, xi) to specificities in other respects than structure. My study of the distribution of some of the Copepoda led to similar views (Esterly, 1912, p. 328) and this matter has been more recently discussed in papers on the experimental side (Esterly, 1917*a*, 1917*c*).

Other writers have had this point of view as regards the behavior of different organisms in the laboratory and also in nature. Walter (1907) was aware of specific differences in *Planaria*. The same attitude is apparent in the papers of Shelford (1911, 1912, 1914, 1915, and especially 1916) and of Allee (1912, 1913) though those investigators were primarily interested in other phases of behavior. It seems to me, as has recently been pointed out by Patten (1917, p. 267), that the attempt to arrive at blanket explanations is the main reason for the controversy over the nature of the processes involved in orientation. Such problems are primarily of physiological interest, and are therefore of a somewhat different nature than the problem of depth migration. But the general attitude of many investigators has been similar in the two cases, especially as regards the failure to recognize that we must deal with specific differences in behavior before a general law can be determined, if such a thing is at all possible. We cannot tell from studies conducted on a given kind of animal how another sort is going to act. Jennings (1909, p. 315) writes: "The man who, from a knowledge of how the starfish and sea anemone behave in the orientation to light, should attempt to predict how the infusoria behave under the same conditions, would fail completely. More striking still, he who from a knowledge of how Stentor becomes oriented in galvanotropism, should predict how Stentor becomes oriented in phototropism, would likewise fail completely. *Different organisms respond in the same tropisms by different methods of action. . . .*" And again: (p. 324) "Different organisms differ in their behavior and reactions just as they do in their structure." If such statements are true as regards certain matters in the physiology of behavior, they are doubtless equally true as regards their relations between behavior in the laboratory and in nature.

If it is granted that a uniform and relatively simple explanation of the depth migration of the plankton is possible, the first preliminary step is to find out what each species does in nature. The facts about migration can not be explained until they have been ascertained. Then the study of reactions under controlled conditions should follow, and this study should be carried on with different kinds of plankton organisms. It is probable that sooner or later there will be duplications in behavior of different species, so that similar explanations will apply.

The Relations Between Geotropism and Diurnal Migration

When an animal in an experiment ascends it overcomes the influence of gravity that is always acting in the same direction with the same force; when the specimen descends it moves in the direction of the action of gravity. It is difficult to see how differences in distribution can be attributed to reactions to an unvarying agent, and I use the term geotropism to designate movement in a vertical direction or maintenance of position in an upright container. Whether upward and downward movements in a tube are reactions to gravity or not, it is certain that their *direction* is changed as variable factors in the environment are altered. In this sense it is permissible to speak of modification of the geotropism; the intention is to express the fact that direction of vertical movement changes under certain conditions, or that the position maintained in a column of water may vary as surrounding conditions change.

Variations in light intensity are constantly affecting organisms of the plankton. Such alterations are due both to increase or decrease in the amount of light entering the water and to movements that bring the organisms into regions of greater or less intensity, depending upon the direction of their locomotion. Since the source of the light that may affect the animals in the sea is always above, it seems probable that light will act as a directive stimulus. It has been suggested, however, by Franz (1913, p. 264) that organisms in the sea may be stimulated from all sides, even from beneath, by the diffusion of the light, except when they are close to the surface or to the bottom. It seems to me that this is a point worth considering. Is a copepod, for example, when at a depth of one hundred feet, aware, so to speak, that the light comes from one direction? It is possible that the light is so diffused that the external condition may be described as "more light" or "less light" instead of as " light from above." We ourselves have the experience, in a dense fog, of not being able to determine the position of the sun; the intensity of the light is nearly the same all about one, particularly toward the sky.

If, however, an animal at a moderate depth in the sea is stimulated by light from a given direction, it is necessary that a distinction be made between phototropism, as such, and modifications of geotropism that are related to the changes in light intensity apart from changes in direction. Are we dealing with "vertical phototropism" or with changes in the geotropism attributable to variations in the light intensity?

DOES THE GEOTROPISM CHANGE AS THE INTENSITY OF LIGHT VARIES?

It was attempted, in the experiments that have been described, to ascertain whether the direction of movement in a vertical container is different in diffuse light and in darkness. In the latter case it is certain that responses coming under the head of phototropism are excluded, and it seems entirely probable that such reactions are done away with in the former case, as the experiments were conducted.

Let us note, in summary, the results of observing behavior in a column of water in darkness as compared with diffuse light.

In *Acartia tonsa* surface specimens go up in the light and down in darkness; animals from deep water are positively geotropic under both conditions. *Calanus* and *Eucalanus* are always positive in darkness as well as in diffuse light. In *Labidocera* some specimens are negatively geotropic in darkness and positively geotropic in diffuse light; but this sort of behavior was not apparent in all sets of animals. *Metridia* shows very strong positive geotropism in diffuse light and in darkness. *Sagitta* is positively geotropic in brighter diffuse light, but in more subdued light and in darkness it is negative.

So far as these experiments are concerned *Calanus, Eucalanus,* and *Metridia* do not show alterations in geotropism as the light intensity changes. A change is very clearly shown, however, in the behavior of *Sagitta* and of some specimens of *Acartia,* though in the latter case the habitat has some relation to the behavior. It is evident, therefore, that change in geotropism because of change in light intensity does not account for the vertical migration in most cases, on the basis of these experiments.

DOES THE GEOTROPISM CHANGE AS THE DIRECTION OF LIGHT VARIES?

Sagitta and surface specimens of *Acartia* move toward a source of light above or below. All the others show a tendency to move *away* from the light whatever its position, when direction of rays is the only factor that is altered. This tendency to move from the light is more marked in some forms than in others. That is, two out of six species move toward the source of light while four move from it; or, the vertical phototropism is positive in two cases, and negative in four cases. It is not allowable, of course, to apply the results of experiments with the light beneath the column to the migration as it occurs

in nature. We come to the conclusion, then, on the basis of the experiments, that the geotropism is usually positive when the light is vertically above the column of water.

DOES THE GEOTROPISM IN DIFFUSE LIGHT AND IN DARKNESS CHANGE AS THE TEMPERATURE AND SALINITY CHANGE?

Plankton animals that perform the depth migrations encounter variations in temperature and salinity as well as in light intensity. It is possible, therefore, that the direction of the vertical movement may be altered as the condition of the water varies. What do the experiments suggest? The tests with *Acartia* are not complete, but it has been shown (Esterly, 1917*b*, table 2 and p. 396) that negative geotropism increases in darkness if the water is 16° C or less, as compared with the distribution in warmer water. There is no change in the geotropism of *Calanus* in diffuse light or in darkness coincident with changes in the condition of the water. In *Metridia* there is some evidence that when the temperature is decreased the geotropism in diffuse light changes from positive to negative; the geotropism in darkness is strongly positive in warmer water, and strongly negative in colder. In *Sagitta* there is no reversal of geotropism in cold water, but the animals do not descend into strata of low temperature even when in light of such high intensity that they would otherwise be very strongly positive.

Four species have been tested as regards geotropism in cold as compared with warmer water, and in only one, *Metridia,* is it clear that the geotropism is reversed when the water is cooled.

DOES THE DIRECTION OF VERTICAL MOVEMENT IN DIRECTIVE LIGHT CHANGE AS THE TEMPERATURE CHANGES?

The results of experiments are available for only two species, *Calanus* and *Metridia,* but the former shows some change in behavior while in the latter there is a marked reversal of the geotropism. In water at room temperature specimens of both forms move away from the light, but if in colder water they move toward the light and remain in the part of the container next the lamp. This sort of behavior is much more marked in *Metridia* than in *Calanus.*

Since but two species were used in this sort of experiment the interpretation cannot be very general. The results are suggestive, however, since they show that there is an alteration in the direction of vertical

movement in directive light as the temperature is decreased. It is important to note in this connection that the upward migration in nature does not take place, in general, in the full intensity of daylight; at any rate the accumulation at the surface occurs after dark in most cases. If, therefore, it is found in experiments that there is relatively more upward movement toward a light when the temperature of the water is lower than when it is higher, we ought not to apply this result to natural conditions unless we know that the results of field work are similar to those of the laboratory. Since we find that the upward movement in nature occurs in light of low intensity or in what is practically darkness, we should look to the results of experiments on geotropism in dim light or in darkness if we are to arrive at an explanation of the diurnal habit from laboratory tests.

To What Extent Will Behavior Under Recurrent External Conditions Explain the Diurnal Migration?

The general facts about the diurnal distribution of plankton organisms are these: at night there is greater abundance of a given species at higher levels, less abundance at lower levels; by day the abundance is less at higher levels, and greater at lower levels. One form may have a vertical range from the 100 fathom to the 200 fathom level and another may range between the surface and 100 fathoms. In each case, however, the general statement made above will apply, though it makes the matter of diurnal migration seem much simpler than it really is.

What responses are involved in such varying relations between the distribution of organisms and the environment? Since the vertical movement is rhythmic and corresponds to the change between day and night it is natural to expect that in the laboratory diurnal migration will be simulated as the light intensity changes. The upward and downward phases should take place under artificial conditions that are similar in general, if not in detail, to the natural conditions under which the animals ascend and descend if the laboratory results are to be applicable to the behavior in nature. For instance, the ascent in a vertical tube should take place in darkness if it is known that the species under experiment is most abundant at the surface of the sea during the night. Or, if the animals in an experiment remain at the top of a column of water at 10° C but not at 17° C it would be

unreasonable to hold that low temperature accounts for the negative geotropism under natural conditions, because the mean annual temperature of the surface of the sea is about 17° C. If a species is negatively geotropic in a cylinder of sea water that has been cooled to 10° C it does not necessarily follow that such animals will be found at the surface of the sea when the temperature is 17° C even though they descend to levels where the temperature is 10° C.

In the experiments dealt with here six species of plankton animals were tested. Aside from the metabolic rhythm of *Acartia* and *Calanus* there is but one form, *Sagitta*, which in experiment shows negative geotropism in darkness when the temperature of the water is about that of the surface of the sea during the summer months. Each species was tested in this regard. Even when the geotropism is reversed from positive to negative upon cooling the lower levels of the column of water, it remains to be shown that the animals will ascend and remain at the upper levels if the temperature there is 16° C or 18° C. The copepod *Metridia* is a good example of an animal that has very marked negative geotropism in water of low temperature. It would undoubtedly begin to ascend if the lower ten centimeters of a tube 50 centimeters long were in ice water; it has not been established whether it will continue to move upward under the initial impulse until the top is reached. It is just this point, however, that it is essential to settle so far as the correlation between experiment and habit is concerned. Again, the experiments on *Calanus* lead us to think that these animals will not be found at the surface in large numbers at night, yet we know that they are.

In addition to movements coincident with external changes the physiological rhythm should be considered. Rhythmic behavior in the absence of recurrent changes in light intensity was noted in two species of *Acartia* (Esterly, 1917*b*) and to some extent in *Calanus*. It has not been established whether the same is true of the other species. When there is an inherent tendency to move upward at a certain time of the day although the animals have been in darkness or dim light for hours, it seems evident that there is a possibility of doing away with the difficulties involved in explanations based on reactions evoked by changes in external factors. I believe that the matter of the physiological rhythm is well worth further study. In the case of *Acartia* the rhythm offers an adequate and satisfactory explanation of the ascent, at least, if the results of experiments are applied unquestioningly. But in *Calanus* so few animals in an experiment actually ascend

that the factor of the rhythm seems not to have much importance, though it probably plays some part in the depth migrations.

It is probably not well to pursue further the discussion of the matters in this section because the experiments are not complete. But omission of these points would be unwise because a most essential consideration is involved, namely:

The Relation Between Experimental and Field Work

After what has been said on this topic in other publications from the Scripps Institute (Michael, 1916, Esterly 1917*a*, 1917*c*) it is needless to say much here. It seems to me more apparent than ever that a knowledge of what organisms do in nature is indispensable for an intelligent evaluation of experimental work that is undertaken to obtain a basis for the explanation of behavior under natural conditions. An observer cannot learn what is to be explained except from knowledge of the organisms of his interest in nature. Experiment without field work will lead to error. For example, if it were said, on the basis of experiment, that *Acartia tonsa* would be most abundant at the surface by day and least abundant by night, it would be a perfectly fair statement so far as experiments with surface animals go. Yet we know that the reverse is true in nature. Again, the experimental results with *Calanus* would justify one in saying that this animal shows practically no diurnal movement. But our field results have led to a different conclusion, for if any plankton animal has the habit of diurnal migration this copepod has. If experiments point in one direction and field observations in another I believe that the latter are more trustworthy. As has been said by Michael (1916, p. xii), "Experiments . . . reveal only what transpires in a laboratory and are necessarily incapable of revealing what occurs in nature."

Both field and laboratory work are indispensable and the two should go hand in hand if it is desired to know the natural history of a species. It is practically impossible, however, in many cases to investigate behavior under experimental conditions on account of the size of the animals, trouble in maintaining specimens in captivity, and difficulty in even approaching the conditions of the natural habitat. The last consideration is one of more than passing importance. If it were possible to duplicate nature in the laboratory and then secure the element of experimental control there would be no doubt that behavior in the laboratory would reveal that in nature, in so far as individual behavior can be taken to represent that of a species.

While some conditions can be duplicated in a laboratory it is impossible to reproduce the entire environmental complex, unless it be in the case of a culture of protozoa or organisms like rotifers. This whole matter has been discussed by Hargitt (1912, pp. 51, 52) and one can hardly do better than quote him.

> What right has one to assume that the reactions of an animal taken rudely from its natural habitat and as rudely imprisoned in some improvised cage are in any scientific sense an expression of its normal behavior either physical or psychical? Is it within the range of the calculus of probability that conclusions drawn from observations made upon an animal in the shallow confines of a finger-bowl, but whose habitat has been the sea, are trustworthy? . . . laboratory appliances are indispensable. But at the same time it must be recognised that they are at best but artificial makeshifts whose values, unless checked by constant appeals to nature, must be taken at something of a discount. This must be especially the case with higher organisms. It seems to the writer that until one has been able to place his specimens under conditions approximating the natural, or has at least brought them to a state of semi-domestication . . . he has small right to dogmatize as to conclusions or to make such conclusions the basis of so-called *laws of behavior.*

Burckhardt (1910, p. 200) writes as follows with regard to the artificial conditions that apply in experiments in the diurnal movement:

> Kann eine Glühlampe das Tageslicht ohne weiteres ersetzen? Haben die stark divergenten Strahlen einer so nahen Lampe dieselbe Wirkung, wie die parallelen der Sonne? . . . Darf man vom plötzlichen Andrehen einer Lampe dieselbe Wirkung erwarten, wie vom allmählichen Aufgehen und Aufsteigen des Tagesstirns? . . . Mir persönlich scheint einstweilen immer noch, aussichtsvoller als die Sisyphusarbeit, im Laboratorium natürliche Bedingungen herzustellen, sei die Beobachtung der mannigfaltigen Experimente, die die Natur in den natürlichen Wasserbecken ausstellt. Haben wir das erschöpfend getan, werden uns unsere Kenntnisse auch die Sisyphusarbeit leichter machen.

The statements of Longley (1917, p. 550) may appropriately be referred to in this connection, where he mentions the color changes shown by fishes in tanks as compared with animals under natural surroundings.

There is no doubt that the questions asked by Hargitt and Burckhardt are pertinent. The attitude revealed by such questions will probably lead to another: Of what use, then, is the method of laboratory experiment? The answer will depend largely upon the end that the experimenter has in view. If he is desirous of finding, for instance, what organisms can do, or how sensitive they are to variations in outer factors, the laboratory method is the only one to use. But when the laboratory results are to be used as explanatory of habits in nature it must be said that the experimental method is of little use if it is followed without regard for its obvious limitations.

GENERAL CONCLUSIONS

The results of the experiments have led to the following conclusions of general application:

1. Owing to specific differences in behavior no general explanation of diurnal migration can be given at present. It is suggested by the experiments that each kind of organism will have its own way, so to speak, of performing the vertical movement, as each has its own peculiar responses in the laboratory.

2. There is evidence that the physiological state changes when the animals are removed from the ocean and kept in the laboratory. While this has not been noted for each species, it is necessary to guard against errors in interpretation that may arise through that cause. We should inquire whether reactions under controlled conditions in a glass vessel are similar in kind to those that would be observed if it were possible to have the element of control and at the same time retain the animals under otherwise natural surroundings.

3. It is suggested by some of the experiments that behavior is in some way related to the habitat from which the experimental specimens are obtained. In general it seems highly desirable to use both animals that are obtained in deep water and at the surface, and compare the reactions in the two cases. If this is not done the possibility remains that what is learned about habit from reactions in the laboratory is not characteristic of the species as a whole, but only of the particular specimens tested.

4. Field studies and laboratory investigation are both necessary and supplementary to each other. While studies on reaction possibilities do not require that the natural habits of the animals be known, this knowledge is a necessity when responses are studied in the expectation that they will reveal the reasons for a habit in nature.

5. So far as these experiments go (they are incomplete in many respects) there is apparently no adequate explanation of diurnal migration that can be based on responses to external stimuli except in the case of *Sagitta*. Additional information may make possible the explanations desired for the other species. It appears, however, that change in geotropism with change of light intensity or in temperature is not general enough to be considered as of wide significance.

6. The action of what may be called a physiological rhythm is clearly shown under certain conditions by the two species of *Acartia*.

There is some similar evidence in *Calanus;* but under the experimental conditions it accounts for the vertical movement of only about 20 per cent of all individuals. Whether this factor will appear in other species remains to be ascertained; but it may be of general occurrence and importance in connection with the diurnal movement.

7. While special attention was not given to the study of individual differences in behavior, the work with single animals has suggested that sooner or later experimental zoology may well be definitely concerned with the peculiarities that appear in different individuals of a species, even when all specimens are kept under the same conditions. Individuality manifested itself everywhere, and I believe that there is a fruitful field for study along that line.

In conclusion it is a pleasure to speak of the suggestions and assistance received from the resident staff at La Jolla. The seminars afforded opportunity for discussion, and there were besides many stimulating conversations. Mr. E. L. Michael was unsparing of his time in talking over matters connected with presenting the experimental data, especially as to arrangement in tabular form that will permit of testing probability by statistical methods. Professor Ritter was always ready to listen and advise, and Mr. W. C. Crandall most efficiently managed affairs connected with the business office. Capt. James Ross did the collecting offshore, and his interest and willingness are very much appreciated.

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